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An empirical test of mid-domain effect using Korean ant richness

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ABSTRACT

The mid-domain effect is a diversity theory, which explains prevalent diversity patterns of hump-shape patterns along altitude or latitude gradients. I tested whether patterns of ant species richness along altitudes and latitudes in South Korea can be described by this theory. Ants on 12 high mountains (>1100 m) throughout South Korea (from 33°N to 38°N) were surveyed using pitfall traps at intervals of 200—300 m of altitude. The number of species collected was used to determine the species richness and the frequency (%, collected traps/total traps) was used to determine abundance. The temperatures of the sampling sites were determined from digital climate maps. Species richness of ants decreased monotonically along altitudinal and latitudinal gradients. However, species richness of cold-adapted species (highland species) showed a hump-shape pattern along altitude gradient, which could be explained by the mid-domain effect. Diversity and abundance of ant species was highly associated with temperature, which can explain the monotonic decrease of diversity. Based on these findings, I devised an integrative diversity hypothesis that explains local exclusive diversity patterns (monotonic decrease, hump-shape, and monotonic increase) and global diversity patterns (peaks in the tropical region and gradually decreases towards the poles). This hypothesis predicts the prevalence of a hump-shape pattern in hot regions and is supported by published insect data.

Introduction

Distribution patterns of species and their emergent property (diversity) have long been a core area of ecology, evolution ecology, and biogeography. Accordingly, global variations in diversity have attracted the attention of numerous researchers for more than 100 years (Sanders et al., 2007). Indeed, many studies have been conducted to investigate the mechanisms underlying the variations in diversity, which has enhanced the development of diversity theories (Allen et al., 2002; Colwell and Hurtt, 1994; Hawkin et al., 2003; Lees et al., 1999; MacArthur, 1972; MacArthur and Wilson, 1967; Rosenzweig, 1995; Williams, 1964). However, patterns of species richness along latitudinal or/and altitudinal gradients have been the subject of debate for several decades (Rohde, 1999). It is generally accepted that diversity declines along latitudinal or altitudinal gradients (Allen et al., 2002; Colwell and Hurtt, 1994; Stevens, 1989, 1992) but such declines are not always straightforward. Evidence of mid-elevation (or latitude) peaks (hump-shaped) has been accumulated (Lees et al., 1999; McCoy, 1990; Olson, 1994; Rahbek, 1995). Additionally, an increasing pattern has been observed for insects (McCoy, 1990; Sanders et al., 2003).

Explanations for the diversity patterns along gradients are generally either distribution range based (Colwell and Hurtt, 1994; Lees et al., 1999; Stevens, 1989, 1992), or energy based (Allen et al., 2002). Rapoport (1982) reported that species at higher latitude have greater latitudinal range, and this phenomenon was defined as Rapoport's rule by Stevens (1989). Rapoport's rule was later extended to explain the finding that species at higher altitudes have wider altitudinal ranges (Stevens, 1992). Using these phenomena, Stevens (1989, 1992) devised a theorem to explain the decrease in species richness along latitude and altitude, which was defined as

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Rapoport's rescue effect. Rapoport's rescue effect is one of several diversity theories that explains the decrease in species richness that occurs with latitude and altitude. However, Gaston et al. (1998) reported that patterns of species richness explained by Rapoport's rule were a local phenomenon that were primarily expressed in Palaearctic and Nearctic ecozones above latitudes of 40—50°N.

When Colwell and Hurtt (1994) developed one-dimensional stochastic models of species richness to explain Rapoport's rule, they unexpectedly found that the pattern of species richness within a domain produced a hump-shaped curve that declines symmetrically from the center towards the edges of the domain. This phenomenon was termed the mid-domain effect and has been used to explain the gradual decline of diversity that occurs from the equator to the poles without assumption of impacts of abiotic or biotic factors. In the mid-domain effect, the stochastic process of geographical ranges within geometric constraints can lead to the development of species gradients in the absence of any environmental or historical gradients (Colwell et al., 2004). However, the applicability of the use of the mid-domain effect on the basis of theorem or empirical data has been the subject of debate (Zapata et al., 2005). Thus, both theories are used to explain one of the complex patterns. Specifically, Rapoport's rescue effect is used to describe the monotonic decline of local diversity, whereas the mid-domain effect is used to describe the hump-shaped pattern. However, the monotonic increase that occurs along altitude has yet to be explained. Therefore, three exclusive patterns of species richness are not properly explained by currently available theories.

Ants, which are abundant and diverse, have a well-developed taxonomy and are easily sampled throughout the active season of insects almost anywhere worldwide (Hölldobler and Wilson, 1990; Kaspari et al., 2003); therefore, they are useful for testing ecological theories (Sanders et al., 2007) and monitoring influences of environmental change (Agosti et al., 2000). Whereas altitudinal and latitudinal species richness gradients mirror each other, the distributional ranges of species on these two gradients exhibit similar patterns (Stevens, 1992). Despite extensive studies of patterns of species richness along altitude or latitude, only a few field studies on the patterns of species richness along both elevation and latitude gradients are known to have been conducted to date. This study was conducted to identify patterns in ant species richness along these two gradients in South Korea, and to test whether the patterns of ant species richness were subject to the mid-domain effect. Because this theory could not properly explain the observed patterns, I tried to explain the local diversity patterns of ants based on the observed abundance patterns of ant species along altitude.

Materials and methods

Sampling sites

This study was conducted on 12 high mountains (>1100 m) in South Korea (Appendix 1). The mountains were selected to represent latitudinal gradients of species richness of ants from 33°N to 38°N. Four to seven sampling sites were selected from the base to the top of each mountain with an interval of 200—300 m in elevation. The undisturbed forests or grasslands/bushes (mountain tops) were selected as sampling sites to remove the effects of disturbance. Sampled forest sites were composed of trees older than 30 years and well-grown understory vegetation. Of 64 sampling sites, 44 sites are deciduous forest, nine sites are coniferous forest, and 11 sites are bush/grassland (Appendix 1). The details regarding the climate, vegetation, and topography in Korea are shown in Kwon et al. (2011).

Ant sampling and identification

Ants were collected in pitfall traps consisting of a plastic cup (depth 6.3 cm, diameter 8.5 cm). Ten pitfall traps were buried at each sampling site for 10 days during the summer (July—August). Ant foraging is the most active during the survey period (Kwon, 2010b) because this period is the warmest in a year. One to four mountains were surveyed each year from 2006 to 2009 (Appendix 1). Each of the traps was placed 5 m apart from adjacent traps along a line, and approximately one-third of it was filled with polyethylene glycol as a preservative.

Ant specimens were identified using taxonomic keys (JAID, 2010). Ants except Myrmica and two species of Lasius were identified to the level of species or morphospecies. The anatomical characters used for Myrmica identification are too vague to be used for species identification by non-taxonomists. Hence, all Myrmica ants were identified as a species group (Myrmica spp.). Lasius japonicus and Lasius alienus were the most common and abundant among Lasius species. However, an intermediate form of two species was frequently found, and the two species and their intermediate were treated as a species group [Lasius spp. (japonicus + alienus)]. All specimens were deposited in the Insect Laboratory of the Korea Forest Research Institute (Seoul, Korea).

Estimating the temperature of sampling sites

During the preliminary analysis of ant distributions in 243 forests throughout South Korea, temperature was a key factor associated with ant distribution, and other factors such as rainfall and productivity (e.g. Normalized Difference Vegetation Index) were negligible (Kwon, 2010a). I used digital climate maps (Yun, 2010) produced by the Korea Meteorological Administration and National Center for Agrometeorology to extract the thermal parameters for each sampling site. Mean, maximum, and minimum air temperature were estimated based on observation data collected from 1971 to 2008. The spatial resolution of the gridded climate data was 30 m.

Analyses

The number of species of ants that were collected at each sampling site was used to determine the species richness. The frequency (%, 100 × each species collected traps/10 traps) was used to determine the abundance of each ant species at a site. The species richness predicted by the mid-domain effect was estimated using the null model described by Colwell (2006). The average of the predicted values was used for analysis. Regression analysis or correlation analysis was used to identify associations between the parameters.

Results

Through ant surveys of 12 mountains, 4246 ants belonging to 28 species were collected (Table 1). The Myrmica spp. was the most abundant, accounting for 49% of total ants, being found at 53 of 64 sampling sites. Singleton species (collected at a sampling site) were seven species. The range and midpoint of the annual mean temperature of the sampling sites at which each species was collected are given in Table 1. Figure 1 shows the species richness along elevation gradients in 12 mountains. Monotonic decreases in species richness along altitudinal gradients occurred on eight mountains, and mid-elevation peaks occurred on four mountains. However, in the latter, peaks occurred at lower elevations than the peak elevation predicted by the mid-domain effect. Thus, the typical