



# Diversity and distribution patterns of ants along elevational gradients

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## Abstract

Ants are one of the most successful groups of organisms present in almost all terrestrial habitats on the Earth. The published papers on ants with various sampling techniques were reviewed focusing on species richness along the elevational gradients to explain distribution patterns of ants and their potential drivers in the world. Pitfall trapping, hand collection, Winkler extractor and bait traps were found common sampling techniques for ant studies. Based upon literature, five broad distributional patterns were identified viz. mid-elevation peaks, decreasing, increasing, low plateaus, and constant patterns along the elevation ranging from 0 to 4800 m above sea level. The mid-elevation peak was a common pattern. However, ant species richness of Nepal follows a decreasing pattern based on the available records. Temperature was found as the major predictor of species richness patterns of ants.

**Keywords:** Altitudinal diversity, Formicidae, Mid-elevation, Species richness, Temperature

## 1 | Introduction

Ants (Family: Formicidae) are one of the most successful groups of organisms, present in all the terrestrial ecosystems of the earth. This group contains an estimated 30 percent of terrestrial animal biomass and more than 20,000 species (Holl Dobler & Wilson 1990). Currently, there are 17 extant subfamilies, 337 genera and 13,806 species (Bolton 2020). Over 87% of the ant species described fall under four subfamilies viz. Myrmicinae, Formicinae, Ponerinae and Dolichoderinae (Guenard 2013). The oriental region has a peak of overall generic and endemic diversity of ants, most likely species diversity too (Guenard et al. 2012, Guenard 2013). The tropical countries contain the highest diversity of ants and species richness tends to decline both with increasing latitude and altitude (Guenard 2013). However, tropical regions of Africa were less diverse than the regions with similar latitude in Australasia or Neotropics (Guenard et al. 2012). Sanders (2002) observed a decreasing pattern with the maximum ant species richness at lowland habitats; however, others have reported maximum richness at mid-elevation habitats (Smith et al. 2014, Nowrouzi et al. 2016, Flores et al. 2018). A mid-elevation peak is the most typical (50%) of altitudinal species richness pattern, but a decreasing pattern (25%) has also been frequently reported (Rahbek 2005). The highest elevation record of an ant

species (*Formica picea lochmatteri* Starke, 1935) is 4800 m in the Himalayas (Weber 1943). Whatever the case may be, the species richness in higher altitudes (above 1500 m) tends to decline sharply with increasing altitude. Reasons for the decline in species richness at high altitude include increasingly unfavorable environments and the reduced available surface area, primary productivity and resource diversity (Lawton et al. 1987). Mid-elevation peaks may be described by the "ends are bad" and the "middle is good" processes (McCoy 1990). These processes highlight the roles of environmental constraints and the availability of resources upon the distributions of populations. The global ant elevational diversity patterns appear more complex than those of many vertebrate taxa, and they are further influenced by multiple drivers (Szewczyk & McCain 2016). Flores et al. (2018) suggested that drought conditions at low elevations and cold temperatures at high elevations prevent the richness at both extremes of elevational gradients in the Mediterranean mountains. The key hypotheses to explain these broad-scale diversity gradients are based on temperature, water availability, productivity, area, geometric constraints and plant diversity (Peters et al. 2016).

Based on published records, there are 202 species of ants in the Himalayan region with 35% of them (71 species) which are

endemic (Bharti 2008). The first comprehensive list of Nepalese ants by Collingwood (1970) listed 34 species collected from 830 m to 4550 m asl. In Nepal, altogether 127 nominal species of ants are known, however, the species number varies according to different publications (such as Antweb 2020, Thapa 2015, Collingwood 1970). An updated checklist and taxonomic status of known ant fauna of Nepal dealing with taxonomic inconsistencies and species distribution is under the preparation of the first author. Ant distribution patterns in Nepal are important due to Nepal's presence in the center of the Himalayas and it having the highest elevational gradient in the world. The elevational gradient studies on plant species of Nepal show the species richness increases up to 2500 m but the endemism of narrow range vascular plants reach a peak around 4000 m (Vetaas & Gryntes 2002).

This global-scale study is based on the selected literatures from different continents and available elevational records of Nepalese ant species showing the distributional patterns of ants along elevational gradients.

## 2 | Methods

The cited published papers were searched using keywords 'ant' with 'elevation', 'elevational', 'altitude', 'altitudinal', 'species richness' and 'diversity' using the Google scholar search engine. These keywords were searched in the ScienceDaily for recent research news. Furthermore, published original papers were also

obtained from AntWeb, AntCat and AntWiki. Ant literature available in the English language, from 1943 to 2020, dealing with an elevation range up to 4800 m asl across the globe were reviewed. The reviewed papers include studies about areas spreading from the Equator to both the Northern and Southern hemispheres. The majority of these papers, nevertheless, dealt with the Northern hemisphere. Based on the review of papers on ant distribution patterns, survey methods used and the drivers of ant diversity (if noted) were highlighted. For depicting the ant species richness pattern in Nepal, the available elevational records of Nepalese ants were used.

Table 1. Diversity patterns of ants and survey methods in elevational gradient studies

Diversity pattern	Study site/s	Altitudinal range (m)	Survey method/s	Reference
Mid Elevation Peak (MEP)	Panama	300 – 2020	WE, PT	Olson 1994
	Philippines	250 – 750	PT, HC	Samson et al. 1997
	Madagascar	400-1950	LS, PT	Fisher 1998
	South Africa	0 - 2000	PT	Botes et al. 2006
	USA	594-1673	WE, MT, PT	Lessard et al. 2007
	India	300-1650	WE, BTF	Sabu et al. 2008
	India	500 – 4000	PT, LS, SB, SC, BT, HC	Bharti et al. 2013
	Southern Africa	900 -3000	PT	Bishop et al. 2014
	North Western Costa Rica	7 - 1500	PT, WE, BT, HC, MT	Smith et al. 2014
	Australia	100 –1,300	BT, WE	Nowrouzi et al. 2016
	Central Spain	685 – 2390	PT	Flores et al. 2018
	Costa Rica to Mexico	20-2600	BT, S, SB	Longino et al. 2019
Panama and Costa Rica	30 – 2600	WE	Longino and Branstetter 2019	
Decreasing with Elevation (DWE)	Eastern Madagascar	785 – 1680	WE, PT, HC	Fisher 1996
	USA	379-1742	WE	Sanders et al. 2007
	Borneo	580 - 1520	WE, GS	Malsch et al. 2008
	Montenegro	100 - 1900	HC	Karamen 2011
	USA and Australia	350-3000	Literature	Machac et al. 2011
	Australia	300-1100	LS, BF, HC	Burwell and Nakamura 2011
	Malaysia	300 - 1100	PT	Yusah et al. 2012
	Andorra and France	1000 – 2300	PT, HC	Bernadou et al. 2013
Eastern Himalaya	600 -2400	PT, WE	Marathe et al. 2020	
Low Plateau (LP)	Southeastern Brazil	800-1500	BT, HC	Araujo and Fernandes 2003
	Austria	400 – 3312	MR	Glaser 2006
Increasing with Elevation (IWE)	Venezuela	70 - 598	PT, HC	Perez-Sanchez et al. 2013
Constant	Gabon	110 - 640	LS, SB, YPT, PT, MT, HC	Fisher 2004
	Egypt	90 - 1730	PT	Orabi et al. 2011
MEP and LP	Costa Rica	50 – 2000	WE	Longino and Colwell 2011
IWE and MEP	U.S.A.	900-2500	PT	Sanders et al. 2003
MEP and DWE	Tanzania	860-4390	SBE	Peters et al. 2014
	China	800-3200	PT, GS, MT, BF, BTF	Fontanilla et al. 2019
-	Eastern Switzerland	1800-2550	HC, PT	Reymond et al. 2013
-	South Korea	800 - 1577	PT, BT	Kwon 2016

**Survey methods** (BT: bait traps; BF: canopy or bark fogging; HC: hand collection; LS: litter sifting; MT: malaise traps; PT: pitfall traps; MR: museum records; WE: Winkler extractor; S: sweeping; YPT: yellow pan traps; BTF: Burlese-Tullgren funnel; SB: stick beating; SBE: standardized bait experiment, SC: soil cores, GS: general search)

### 3 | Results and discussion

#### 3.1 | Ant distribution patterns along elevation gradients

Global diversity and distribution patterns of ants are yet to be well-understood. In general, five broad patterns of ant elevational diversity were recorded from selected literatures:

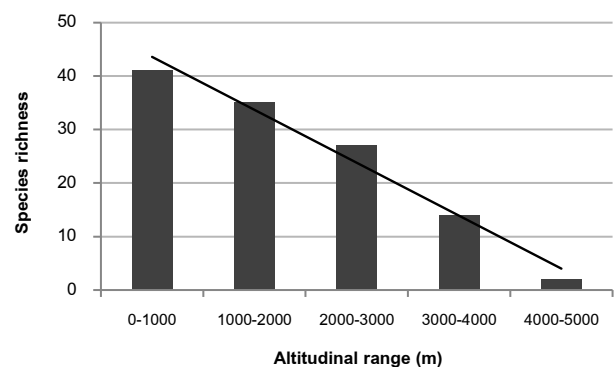
- i. Decreasing patterns (the highest diversity in the lowest elevation),
- ii. Low plateaus (high diversity across the lowest elevation up to 300 m),
- iii. Mid-elevation peaks (highest diversity at middle elevations above 300 m from the base),
- iv. Increasing patterns (increasing diversity with increasing elevation), and
- v. Constant (none of the above definitions).

Diversity patterns of ants and survey methods used in selected elevational gradient studies have been summarized in the Table 1. Studies have shown that out of the five patterns of ant diversity along elevation gradients, the two commonest patterns were the mid-elevation peak and decreasing patterns. The mid-elevation peak pattern was most common with nearly 51% of the studies – ranging up to 4000 m – followed by a decreasing pattern with nearly 33% of the studies – ranging from 100 m to 4390 m (Table 1). Higher species richness at mid-elevations is because of climatic severity in the higher or lower elevations and the availability of limited resources at higher elevations (McCoy 1990). Generally, low elevations are too hot except for winters, and higher elevations are too cold or frigid throughout. The highest productivity at mid-elevations is due to the presence of higher photosynthetic and lower respiratory rates (Janzen 1973) which results in the hump-shaped pattern of species distribution. Species richness decline monotonically with increasing altitude because of reduced temperature and consequent decreased productivity which is often thought to reflect the latitudinal gradient (Rahbek 1995, 1997). However, the patterns of species richness may be different within or between taxa at low and mid-elevations and also between different regions or within areas on a regional scale (Rahbek 1995).

Species richness was the highest at the lowest elevation of the southern slope and again at the mid-elevation of the northern slope of Soutpansberg Mountain, South Africa (Munyai & Foord 2012). Peters et al. (2014) observed species richness at a mid-elevation peak in managed ecosystems while a decline with elevation was seen in natural ecosystems. Sanders et al. (2003)

suggested that species richness for some taxa may be the highest even at high altitudes in arid ecosystems. In such ecosystems, lower temperature and higher precipitation may support higher primary productivity and cause low levels of physiological stress. Variations in diversity patterns may also be dependent upon the sampling and scale of the study. However, no specific trends in species distribution have been identified either continent-wise or the hemisphere-wise.

Available elevational records of Nepalese ants from 200 m to 4550 m were used to extrapolate the species richness pattern along an altitudinal gradient in Nepal (AntWeb 2020, Thapa 2015, Collingwood 1970). The data showed that the species richness of Nepalese ants follows a decreasing pattern (Figure 1). However, most of the areas of Nepal are still unexplored and it is difficult to generalize ant distribution patterns with the few collections and limited published information on Nepalese ant species.



**Figure 1.** Ant species richness pattern along altitude in Nepal (N= 83 species) ( $y = -9.9x + 53.5$ ,  $R^2 = 0.9774$ )

The ant surveys representing most of the sampling techniques viz. pitfall traps, Winkler extractor (litter sifting), bait traps, hand collection, canopy or bark fogging, malaise traps, sweeping, yellow pan traps, Burlese-Tullgren funnel, stick beating and soil cores were used for assessing the ant species richness along elevation gradients (Table 1). The most frequently used survey method in the ant inventory was the pitfall trap method followed by litter sifting and Winkler extractor, hand collection, and the bait traps. The majority of the studies used two or more methods for the collection of ants while some studies used a single method viz. pitfall trap or Winkler extractor. It is more or less obvious that use of multiple methods are likely to produce better results.

### 3.2 | Drivers of ant diversity

Temperature has been described as a prominent driver (Bernadou et al. 2013, Sanders et al. 2007, Malsch et al. 2008) or the most important predictor (Longino & Colwell 2011, Bishop et al. 2014, Machac et al. 2011) of species richness. Relative humidity, soil nutrients, elevation-specific regional area, and the mid-domain effects were reported to have comparatively less impact on ant species richness (Longino & Colwell 2011). Species richness is also influenced by different sets of variables among the individual taxonomic groups but temperature is the most important in the majority of taxa (Peters et al. 2016). Marathe et al. (2020) suggested that elevational richness patterns are driven by a combination of climatic and geometric constraints. Variation in ant species richness over the elevational gradient was partially explained by climate (Sanders et al. 2003) and was influenced by the presence of favourable physical conditions and the prey resources (Sabu et al. 2008). Decline in species richness is correlated with decreasing temperature, high humidity, scarcity of nesting places and nutritional resources (Malsch et al. 2008). Local habitat features like sun exposure, vegetation density, surface moisture (Bernadou et al. 2013, Munyai & Foord 2012, Araujo & Fernandes 2003), vegetation types (Lasmar et al. 2020), types and number of nutrients (Peters et al. 2014) and available areas (Bishop et al. 2014) also influence species diversity. Elevation influences the changes in ant communities often due to increased moisture availability (MontBlanc et al. 2007).

## 4 | Conclusions

The review concludes the mid-elevation peak as a common species richness pattern followed by a decreasing pattern. Other patterns include increasing pattern, low plateaus and constant. The majority of the studies reported temperature as the important driver of diversity. Pitfall traps, Winkler extractors, hand collection and bait traps are found common ant survey methods. Based upon available elevational records, the species richness of Nepalese ants shows a decreasing pattern. Further systematic surveys and inventories of unexplored areas representing wide elevation range can provide the picture of real distribution pattern of ant species in Nepal.

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## Authors' contributions

Subedi, I. P. conceived the study and analyzed the data; both authors wrote the manuscript.

## Conflicts of interest

Authors declare no conflict of interest.

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