

## DOES $\beta$ -DIVERSITY ALLOW RELIABLE DISCRIMINATION BETWEEN DETERMINISTICALLY AND STOCHASTICALLY ASSEMBLED COMMUNITIES?

Armin Götzke & K. Eduard Linsenmair

Zoologie III, Theodor-Boveri-Biozentrum der Universität, Am Hubland, D-97074 Würzburg, Germany

*Key words:* Ant mosaics,  $\beta$ -diversity, species diversity, tropical arthropod communities.

### Tropical communities and the use of $\beta$ -diversity

Many tropical communities are very rich in species, exceeding by between 3 times and 3 orders of magnitude the number of species per taxonomic unit in comparable temperate systems (e.g., Wilson 1988). The mechanisms maintaining this high diversity are little understood (Linsenmair 1990, 1995; extensive reviews in Huston 1994 and Rosenzweig 1995). Deterministic models are based on the niche concept, proposing that more species are able to live in the tropics because there is a higher density of niches in a given area. A greater number of niches per area implies more resources and/or smaller niche breadth for the average species, leading to a high proportion of specialists. Since identical habitats offer the same set of resources, and since each species is considered - within the framework of this concept - capable of outcompeting any other species in its particular niche, the species composition of identical habitats should be the same or, at least, very similar. The stochastic view, on the other hand, stresses the importance of unforeseeable disturbances preventing the competitive exclusion principle from ever becoming fully effective. In the stochastic models several species may depend on the same limited resource without automatically coming into competition, since none of these species will succeed in finding all suitable habitats during the time available for settling. Therefore, the species composition of identical neighboring habitats is expected to differ considerably (see Chesson & Case 1986 for an overview of the different concepts).

The term " $\beta$ -diversity" was originally introduced to denote and quantify temporal differences in species composition of the same habitat (Whittaker 1960). Today, however, the term " $\beta$ -diversity" is predominantly used to describe differences (or similar-

ities, one being just the complement of the other) in the species composition of habitats at different, especially neighboring locations (Shmida & Wilson 1985). In order to mathematically describe the level of similarity, several indices have been developed. There are binary indices, which use only presence/absence data, and there are non-binary indices, which also take the relative abundance of a species into account. In order to obtain a suitable measure of comparison, "normalized" indices were introduced. The resulting similarity values range from 0 (no species in common) to 1 (all species in common, and their respective relative abundances identical) (see Janson & Vegelius 1981, Wolda 1983, and Magurran 1988 for critical discussions of various indices).

The following considerations are based on non-binary, normalized indices of similarity.

### Tropical arboreal ant communities as test systems

Many of the hitherto investigated ant communities are known to reveal strict dominance hierarchies and characteristic species assemblages (Hölldobler & Wilson 1990). These findings suggest that deterministic forces act in structuring these ant assemblages. If so, the model would predict low values of  $\beta$ -diversity between ant communities in identical habitats. However, we suggest with the following considerations that in tropical arboreal ant communities a mainly deterministic structure is not necessarily correlated with low values of  $\beta$ -diversity.

A common pattern in numerous arboreal ant communities is the so-called "ant mosaic" (e.g., Room 1971, Leston 1978, Adams 1994; reviews in Jackson 1984 and Majer 1993). Ant mosaics are characterized by a few dominant species occupying mutually exclusive territories. Each of these dominant species has a particular associated set of subdominant

species, because the subdominant species can only co-exist with one or two dominant species. This model would predict that habitats/assemblages dominated by the same species are more similar in their composition and show lower values of  $\beta$ -diversity than those dominated by different species.

A mathematical description of  $\beta$ -diversity in this system can be formulated making the following assumptions:

- 1) The ant communities occur in physically separated habitats; examples may be islands or tree crowns.
- 2) Territory boundaries of the dominant species coincide with the habitat boundaries, and each territory is restricted to one habitat.
- 3) There is no free habitat; all habitats are colonized by one of the dominant species.
- 4) We distinguish two types of comparisons: on the one hand are comparisons of communities structured by the same dominant species (type A), and on the other those of communities structured by different dominant species (type B). All comparisons of type A have a value of similarity of  $a$ , and the comparisons of type B a value of  $b$ , with  $a, b \in [0;1]$ , and  $a > b$ .

Then, with  $n$  dominant species, and  $p_i =$  relative abundance of the dominant species  $i$  ( $i \in [1,n]$ ), the

mean value of  $\beta$ -div can be calculated according to the formula:

$$(1) \beta\text{-div} = 1 - \{(p_1^2 \cdot a + p_2^2 \cdot a + \dots + p_n^2 \cdot a) + (p_1 \cdot (p_2 + p_3 + \dots + p_n)) \cdot b + (p_2 \cdot (p_3 + p_4 + \dots + p_n)) \cdot b + \dots + p_{n-1} \cdot p_n \cdot b\},$$

or

$$(2) \beta\text{-div} = 1 - \{a \cdot \sum p_i^2 + b \cdot \sum p_i \cdot (p_{i+1} + \dots + p_n)\}, \text{ for } i = 1 \text{ to } n.$$

In addition to  $a$  and  $b$ , the following variables influence the  $\beta$ -div value:

- I) the number of dominant species in the system, and
- II) the distribution of the relative frequencies of the dominant species.

I) The number of dominant species in the system.

Let us assume that the relative abundances of the dominant species are equal, with  $p_1 = p_2 = \dots = p_n = 1/n$ .

Then, equation (2) changes to  $\beta\text{-div} = 1 - \{a/n + b/2 \cdot (1 - 1/n)\}$  (3), in which  $\beta$ -div is a function of  $n$ . Obviously,  $\lim_{(n \rightarrow \infty)} \beta\text{-div}$  equals  $1 - b/2$ . Therefore, with growing  $n$ ,  $\beta$ -div approaches a value of  $1 - b/2$ .

To give an example: let  $a = 0,8$  and  $b = 0,2$ . Then, equation (3) changes to

$\beta\text{-div} = 0,9 - 0,7/n$  (4); the corresponding graph is shown in Fig.1. Under the conditions described,  $\beta$ -div reaches a value of 80% with  $n = 7$  species.

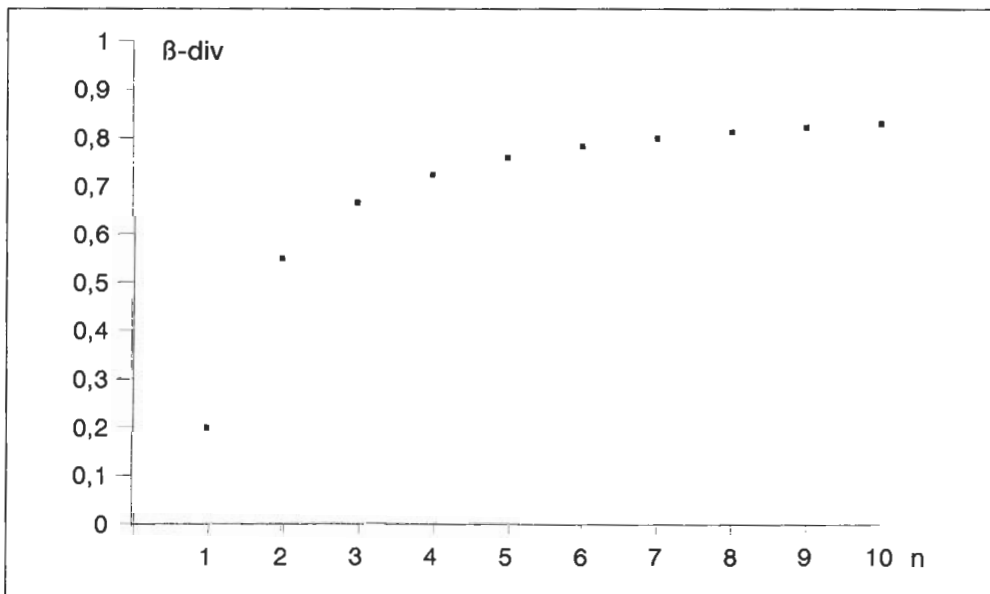


FIG.1. Development of  $\beta$ -div in relation to the number of structuring species  $n$  (with  $a = 0,8$  and  $b = 0,2$ ).

II) Distribution of the relative frequencies of the dominant species.

It can be shown that  $\beta$ -div reaches its maximum if their relative abundances are equal, with  $p_1 = p_2 = \dots = p_n = 1/n$  (see Appendix).

To give an example: we assume a system of two dominant species. In one case, the relative frequency of species I = species II = 0,5; in the other, the relative frequencies are 0,9 and 0,1. Additionally, let  $a = 1$  and  $b = 0$ . As a result, in the first case  $\beta$ -div calculates to

$$1 - (2 \cdot 0,5^2) = 0,5, \text{ and in the second to}$$

$$1 - (0,9^2 + 0,1^2) = 0,18.$$

Therefore, under these circumstances  $\beta$ -div develops analogously to the diversity of the dominant ant species. With a growing number of species, and growing equality in their relative frequencies,  $\beta$ -div approaches its maximum, which is  $1 - b/2$ .

### Conclusion

Ant mosaics are a special form of species assemblage, so far unknown in other arthropod taxa. However, some studies suggested that the structuring influence of the dominant ant species extends to other arthropod species and even plants (Leston 1973; see Majer 1993 for an overview). Therefore, if dominant ant species in the tropics exert strong structuring effects on the species composition of entire arthropod communities, high values of  $\beta$ -diversity may result and yet be due to processes with a strong deterministic component. However, we want to emphasize that the colonization of free habitats by dominant species may happen in a stochastic way, resulting in an advantage in colony growth for that species that succeeds in establishing first. This advantage prevents this species and its associated community from being eliminated by potentially competitively superior species. Therefore, though deterministic processes control community development after a free habitat has been colonized by a dominant species, the initial event of finding a free habitat may be of particular importance for the composition and diversity of the whole local community.

Recent studies of arthropod communities in dipterocarp rainforests in Borneo revealed no evidence for the existence of ant mosaics (Floren & Linsenmair, in press, and Götzke & Linsenmair, in prep.), but instead suggest that no fixed species patterns occur. Additionally, one should note that most reported ant mosaics occurred in plantations, dis-

turbed forests and mangrove, i.e., in habitats that probably harbor impoverished ant faunas. Hölldobler & Wilson (1990) suggest that the establishment of dominance hierarchies is only possible in species-poor faunas ("dominance-impooverishment-rule"). Therefore the existence of ant mosaics in tropical arboreal communities of plantations, mangrove etc., may be possible because these communities contain relatively few species. In species-rich systems, as seems to be the case for the arboreal communities of tropical lowland rainforests (Wilson 1987; Floren & Linsenmair, in press.), things might be different. However, Leston (1973) states that the observed ant mosaics in cacao plantations also occur in primary forests, though in a more complex form. In future studies, the possibility of structuring processes leading to, and resulting from ant mosaics should be taken into consideration to avoid misjudging the relative roles played by deterministic and stochastic factors when drawing conclusions from high values of  $\beta$ -diversity.

### APPENDIX

The function (2)  $\beta$ -div =  $1 - \{a \cdot \sum p_i^2 + b \cdot \sum p_i \cdot (p_{i+1} + \dots + p_n)\}$ , for  $i = 1$  to  $n$ , under the constraints

$$0 \leq p_i \leq 1, \text{ and } \sum p_i = 1,$$

reaches its maximum at  $p_i = 1/n$ ,  $i = 1, 2, \dots, n$ , because then  $y(p_i) = \sum p_i^2$  (I) as well as  $z(p_i) = \sum p_i \cdot (p_{i+1} + \dots + p_n)$  (II) is minimal under the same constraints. This is shown in the following, using Lagrange multipliers: (I): Instead of  $y(p_i) = \sum p_i^2$ , we examine the function  $y(p_i, \lambda) = \sum p_i^2 + \lambda \cdot (\sum p_i - 1)$ . To obtain its minimum, we have to form the partial derivatives for all variables, resulting in

$$dy/dp_i = 2p_i + \lambda,$$

$$dy/d\lambda = \sum p_i - 1, \text{ with } i = 1, 2, \dots, n$$

If these derivatives are equal to 0, then  $p_i = -\lambda/2$ ,  $i = 1, 2, \dots, n$ .

This is equivalent to the statement that all  $p_i$  are equal if  $y(p_i) = \sum p_i^2$  attains a relative minimum.

(II): analogous to (I), we use the Lagrange approach, resulting in the partial derivatives

$$dz/dp_i = 1 - p_i + \lambda, \text{ and}$$

$$dz/d\lambda = \sum p_i - 1, \text{ with } i = 1, 2, \dots, n$$

The first derivatives equal 0 for  $p_i = \lambda + 1$ ,  $i = 1, 2, \dots, n$ . Again, if the function  $z(p_i)$  has a relative minimum, then all  $p_i$  are equal.

Neither (I) nor (II) can have its absolute minimum at a boundary point of the domain, which is given by the constraints. This may be shown by com-

parison of function values for boundary points and suitable neighboring points in the interior of the domain. The functions - being continuous in the variables  $p_i$  - take their absolute minimum on the bounded and closed domain. As we have seen, this can happen only at an interior point in the domain and therefore all the partial derivatives must be equal to 0 at such a point. Now, since  $(p_1, \dots, p_n) = (1/n, \dots, 1/n)$  is the only point where all these derivatives vanish, both functions take their absolute minimum at this point. Therefore  $(p_1, \dots, p_n) = (1/n, \dots, 1/n)$  is also the unique point where the function

$1 - \{a \cdot \sum p_i^2 + b \cdot \sum p_i \cdot (p_{i+1} + \dots + p_n)\}$ , for  $i = 1$  to  $n$  (for arbitrary positive constants  $a$  and  $b$ ) has its absolute maximum, the value of which is  $1 - a/n - b \times (n-1)/2n$ .

#### ACKNOWLEDGEMENTS

We thank Prof. Dr. Herbert Vogt for essential support concerning the mathematics, and Konrad Fiedler and Barbara König for critical comments on the manuscript. This work was supported by grants from the Deutsche Forschungsgemeinschaft (Li 150/13 1-3).

#### REFERENCES

- Adams, E. S. 1994. Territory defense by the ant *Azteca trigona*: maintenance of an arboreal ant mosaic. *Oecologia* 97: 202-208.
- Chesson, P.L., & T.J. Case. 1986. Overview: Nonequilibrium community theories: Chance, variability, history, and coexistence. Pp. 229-239 in Diamond, J., & T. J. Case (eds.), *Community ecology*. New York.
- Hölldobler, B., & E. O. Wilson. 1990. *The ants*. Berlin.
- Huston, A. 1994. *Biological diversity. The coexistence of species in changing landscapes*. Cambridge.
- Jackson, D. A. 1984. Ant distribution patterns in a Cameroonian cocoa plantation: Investigation of the ant mosaic hypothesis. *Oecologia* 62: 318-324.
- Janson, S., & J. Vegelius. 1981. Measures of ecological association. *Oecologia* 49: 371-376.
- Leston, D. 1973. Ants and tropical tree crops. *Proc. Royal Entomol. Soc. London, ser. C*, 38: 1.
- Leston, D. 1978. A Neotropical ant mosaic. *Ann. Entomol. Soc. Am.* 71: 649-653.
- Linsenmair, K. E. 1990. Tropische Biodiversität: Befunde und offene Probleme. *Verh. Dtsch. Zool. Ges.* 83: 245-261.
- Linsenmair, K. E. 1995. Tropische Biodiversität - vom ursprünglichen Verständnis der strukturellen und funktionellen Komplexität noch weit entfernt. *Rundgespräche d. Kommission f. Ökologie*, Bd. 10, pp. 115-126.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton.
- Majer, J. D. 1993. Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia - its structure and influence on arthropod diversity. Pp. 115-141 in LaSalle, J., & I. D. Gauld (eds.), *Hymenoptera and biodiversity*. Wallingford.
- Room, P. M. 1971. The relative distributions of ant species in Ghana's cocoa farms. *J. Anim. Ecol.* 40: 735-751.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge.
- Shmida, A., & M. V. Wilson. 1985. Biological determinants of species diversity. *J. Biogeogr.* 12: 1-20.
- Whittaker, R. H. 1960. Vegetation of the Siskyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279-338.
- Wilson, E. O. 1987. The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica* 19: 245-251.
- Wilson, E. O. 1988. *Biodiversity*. Washington.
- Wolda, H. 1983. Diversity, diversity indices and tropical cockroaches. *Oecologia*, 58: 290-298.

*Accepted 27 August 1996.*