

Correspondence

***'Everything is everywhere, but, the environment selects'*; what did Baas Becking and Beijerinck really say?**

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Citations of the old microbiological tenet *'Everything is everywhere, but, the environment selects'* have spectacularly increased in frequency in recent years in environmental microbiology and are sometimes also quoted in theoretical ecology publications. This citation has been used as the question-raising starting point for studies of prokaryotic and protist biodiversity and their biogeographical patterns (Garcia-Pichel *et al.*, 1996; Zwart *et al.*, 1998; Staley and Gosink, 1999; Cho and Tiedje, 2000; Fenchel, 2003; Finlay and Fenchel, 2004; Lage *et al.*, 2004; Richard *et al.*, 2005). Moreover, the principle expressed by this citation has also been found very useful to focus the intellectual debate on the mechanisms of community assembly where the principle is implicitly used in classical niche-assembly theories, while it is outright rejected by opposing biodiversity theories that claim a major role for dispersal limitation and stochasticity in the assembly of natural communities (e.g. Hubbell, 2001).

The original statement, which is so beautiful and appealing because of its conciseness, appeared for the first time in the written literature in Dutch in the book *'Geobiologie of inleiding tot de milieukunde'* (Geobiology or introduction to the science of the environment) by Professor Lourens Gerhard Marinus Baas Becking (Fig. 1) as *'alles is overal; maar het milieu selecteert'* (italics following the original text on page 15 of Baas Becking, 1934). He developed the statement from two basic rules, which were connected by the word *'maar'* (only word not written in italics), which is the Dutch equivalent of the English coordinating conjunction *'but'*. Its use expresses that the latter connected phrase is contrary to the expectation raised in the former (Collins Dictionary). In this correspondence, we carefully consider what was originally written in the Dutch language by Baas Becking (1934) and by his compatriot and inspirator Beijerinck (Fig. 2) early in the 20th century and show that both scientists formulated concepts that are pertinent for modern studies of the biogeography of microorganisms and of the assembly of natural communities.

Unfortunately, nowadays, we see many citations of Baas Becking (1934) where either the coordinating conjunction *'but'* is missing, i.e. *'everything is everywhere, the environment selects'* or where it is replaced by *'and'*, i.e. *'everything is everywhere, and the environment selects'*. *'And'* also is a coordinating conjunction, although with a completely different meaning. We argue that the use of the coordinating conjunction *'but'* is essential to conserve the original meaning of the statement intended by Baas Becking (1934). It reflects that there is an apparent contradiction between the empirical observations that specific microorganisms are observed in their characteristic environments and the idea that all microorganisms are cosmopolitan. The idea of Baas Becking was that while all microbial life is distributed worldwide, in a given environmental setting most of the microbial species are only latently present. Hence, on a small scale, most microbial biodiversity is hidden for our observation, because most species will occur at densities below our limit of detection. On page 18, Baas Becking (1934) recognizes that this hidden rule to be true requires that microbial germs are transported and distributed homogeneously over the earth. He invokes atmospheric transport and mentions what he calls *'lucht plancton'*, i.e. the microbial germs transported passively by air masses over large distances.

Apart from incomplete translation of the original statement there is also some confusion about its authorship. Most current scientific publications correctly cite Baas Becking (1934), but some confusion has been created by many University teachers attributing this statement to the well-known Dutch microbiologist and founder of the Delft school in Microbiology, Martinus Beijerinck (e.g. Atlas and Bartha, 1992; Wirson, 2004). This confusion has perhaps been created by Baas Becking (1934) himself, since when developing his principle he refers to the two rules of Beijerinck and cites his famous paper on infusions and the discovery of bacteria written in Dutch (Beijerinck, 1913). Nevertheless, a careful reading of that latter paper shows that Beijerinck took an empirical approach, used very wordy language and that the basic concepts of the tenet were only implicit in this publication (Beijerinck, 1913). Moreover, some ideas corresponding to the second part *'the environment selects'* are treated before the concepts



Fig. 1. Professor Lourens Gerhard Marinus Baas Becking in 1935 on board the R.V. 'Max Weber' close to Texel. Photography by H.C.J. Oomen, reproduced from 'Vakblad voor Biologen' (1983), 13, 230–232 with the permission of the NIBI (Netherlands Institute for Biology).

of the first part. Thus, Beijerinck wrote 'wat voor melk geldt is ook in andere gevallen toepasselijk en de nauwkeurige waarneming leert, dat de bewoners der infusies steeds verschillend zijn al naar mate van de levensomstandigheden, die in de infusies zijn verwezenlijkt' (what is true for milk can also be applied to other cases, and from careful observation we can learn that the inhabitants of infusions are always different according the realized living conditions offered by the infusions). Five phrases later Beijerinck (1913) writes '... de ondervinding heeft geleerd dat vele kiemen zoo algemeen in onze omgeving voorkomen, dat als het bovengenoemde vraagstuk maar met voldoende nauwkeurigheid onderzocht wordt, ook dikwijls een scherp antwoord verkregen aangaande den aard der organismen, die onder bepaalde levensomstandigheden in de infusies verwacht of niet verwacht kunnen worden' (... empirical findings have shown that most germs are extremely common in our surroundings, and if the main question is studied with sufficient rigour an answer can be obtained concerning the characteristics of the organisms, which are expected to be present or absent according the environmental conditions in these infusions). Therefore, although the works of Beijerinck certainly were its major source for inspiration, we believe that full credit needs to be given to Baas Becking for the conciseness and the beauty of the original formulation in Dutch of the principle that should be translated into English as follows: '*Everything is everywhere, but, the environment selects*'.

To understand why Professor Baas Becking was modest in this respect and how his thinking and writing were influenced by the works of Beijerinck, it should be realized



Fig. 2. Martinus W. Beijerinck in the late 1920s. He was the first professor of Microbiology at Delft University (1895–1921) and his work and ideas represented a great source of inspiration for L.G.M. Baas Becking. Courtesy of Lesley A. Robertsen, reproduced with the permission of the Delft School of Microbiology Archives at Delft University of Technology, the Netherlands ©.

that Baas Becking admired his compatriot Beijerinck and fully adhered to the methods of the Delft school of microbiology. He started as a student in Delft University and followed the courses by the microbiologist C.B. Van Niel, but later shifted to study biology with a major focus on botany at Utrecht University (the Netherlands). During his research at Stanford University and later at the Marine Laboratory in Pacific Grove (USA) he became fascinated by the study of extreme environments including salt lakes and methane-rich reservoirs in California, which prompted his interest on the biology of the so-called 'lower organisms' and roused his profound recognition and admiration for the earlier work performed by his compatriot Martinus Beijerinck. A succinct bibliography of Baas Becking has been proposed by his former student Anton Quispel (1998), who was professor in plant physiology at Leiden University.

Baas Becking (1934) recognized that the principle he formulated was implicit for the technique of selective culturing (enrichment culturing) employed by the Delft school

of microbiology. Baas Becking (1934) writes ‘het vertrouwen waarmee men steeds ophopings cultures inzet, bewijst dat men deze wet stilzwijgend erkent’ (the trust with which enrichment cultures are set up proves that this law is tacitly accepted). This implies that the latent microbial life can be resuscitated by providing the appropriate environmental conditions as it is practised in carefully designed enrichment cultures in the laboratory. Baas Becking (1934) thus expressed that the enrichment culturing technique potentially reveals the latent microbial world of supposed cosmopolitan character and that testing the capacity of resuscitation of the latent microbial species is therefore essential for proving or rejecting his ideas. Thus, he thought that the enrichment culturing technique provides a look into the ‘hidden reality’ of every microorganism occurring everywhere. Nowadays, we realize that this approach is highly compromised by the fact that only a very minor proportion of prokaryotes can be cultured according to existing methodology (Fry, 1990). On the other hand, despite novel culture-independent approaches including ribosomal gene clone libraries and metagenomic sequencing we realize that it will be practically impossible to obtain evidence for the first part of the tenet ‘everything is everywhere’, because of detection limits and the long-time unexpected high number of microbial species (Pommier *et al.*, 2005).

The ideas and concepts developed by Beijerinck and Baas Becking are certainly very useful and some of them appear even remarkably modern in the context of ecological theories on the assembly of natural communities. Unfortunately, this is not fully recognized by the mainstream classical ecology, because macroecology and microbial ecology historically developed into two parallel stems. We argue that both Beijerinck and Baas Becking were clear precursors of the niche concept in ecology and advocates ‘avant la lettre’ of a deterministic niche assembly theory. Nonetheless, both acknowledged that their approach is only pertinent for bacteria, yeasts, protozoa and microscopic algae, the so-called lower organisms according to Baas Becking. In his 1913 paper on the infusions and the discovery of the bacteria Beijerinck recognizes a new branch of science which he called ‘microoekologie’ and clearly corresponds to what is meant by microbial ecology today. Beijerinck (1913) takes a clear deterministic approach when he opposes his point of view against that of Ehrenberg, who had described in his nicely illustrated book of 1838 that the final community composition of infusion experiments largely depended on chance. This shows that neutral theory as nowadays advocated by Hubbell (2001) has perhaps a longer tradition in ecology than niche assembly theories. Baas Becking (1934) also described concepts corresponding to the potential and realized niche as they were proposed 30 years later by Hutchinson (1965) when he writes ‘En

zoo kan men de bestaansmogelijkheden van een organisme omlijnen door kweekproeven in het laboratorium, en zoo kan men dit gebied – het potentieele milieu – vergelijken met het natuurlijke milieu en vinden dat dit laatste nimmer uitgebreider is dan het eerste’ (This way, one can describe the existence possibilities of an organism by culture experiments in the laboratory, and one can compare this space, i.e. the potential milieu, with the natural milieu of the organism and find that the latter is never larger than the former). Baas Becking (1934) also had a profound recognition of the fact that organisms modify their environment and that such phenomena are important on a global scale. Accordingly, he used the word Gaia for his inaugural speech as Professor at the University of Leiden (Baas Becking, 1931) a long time before this word was promulgated by James Lovelock and Lynn Margulis (1974).

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