

Leafhoppers (Hemiptera, Auchenorrhyncha) from the perspective of insular biogeography

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Abstract

Distribution and abundance of leafhoppers (Hemiptera: Auchenorrhyncha) were investigated on the chain of the East Frisian dune islands situated in the Wadden Sea from 3 to 13 km off the north western German coast in order to explore the absence or presence of species on the islands and to explain differences in colonization success of species. - A total of 172 leafhopper species was assessed from the islands by standardized sweepnet samplings from 1982 to 1988. Species numbers found on the 7 old islands are roughly on level (110 to 139 species), but differences in species composition are considerable. The species-abundance relations of the leafhopper assemblages show great similarities to those of dynamic and instable communities. The leafhopper data of the East Frisian islands fit the "habitat-diversity hypothesis" more closely than the "area-per-se-hypothesis" of insular biogeography theory. Colonization success of the potential colonists correlates positively or negatively with certain characteri-

stics, including (1) degree of habitat specialization; (2) preference for special groups of host plants; (3) preference for particular stages of landscape development; (4) degree of niche overlap; (5) abundance in the recruitment area. It is demonstrated that the specific characteristics of each potential colonist species combine to a "disposition" regarding their prevailing colonization chances: high disposition values render a high colonization rate, low disposition values render a low colonization rate.

Key words: Auchenorrhyncha, North West Germany, East Frisian Islands, insular biogeography.

Introduction

Islands are particularly suited for analysing distribution patterns of species assemblages and their dynamic in space and time. Important factors such as size, isolation and age of development are easily determined. Islands are often “more simple“ in structure and their communities of organisms are more easily to survey.

It was not until the sixties of the last century when islands were brought to the attention of ecologists by the “equilibrium theory of insular biogeography“ of Robert MACARTHUR and Edward WILSON (1963, 1967). Their concept, which seeks to explain species numbers of organismic assemblages by the parameters size and degree of isolation of an island in first place, provoked lively debate and extensive conceptual advances that have precipitated in a plethora of publications to the present day (for reviews see CONNOR & MCCOY 1979, WILLIAMSON 1981).

The chain of East Frisian dune islands situated off the central European mainland offer all advantages as study sites:

The islands emerged independently from the mainland, so that all organisms had – and still have – to immigrate. The islands share many features, but do also differ in size, degree of isolation, landscape structure as well as age and state of development. The islands show a characteristic set of well distinguishable habitats on a small scale which themselves can be viewed as “islands“, due to their mosaic-like distribution (“habitat patches“).

In the present contribution, which is largely based on research conducted from 1982 to 1988 (NIEDRINGHAUS 1991), the colonization success of leafhoppers (Hemiptera: Achenorrhyncha) on the dune islands is analysed by comparing potential colonist and assessed species. The following questions are addressed in particular:

(1) How many and which species have successfully colonized the islands and different habitats?

(2) Which role do “area-related“ factors like size, isolation, habitat diversity, age and stage of development of an island play in the process of colonization? How do the present

results fit current theories of “insular biogeography“?

(3) Which role do “organisms-related“ factors (dispersal ability, body size, hibernation, generation cycle, habitat requirements, feeding specificity, etc.) play? Which characteristics can be related to increasing or decreasing colonization chances?

(4) Does the specific set of characteristics of each potential colonist convey a specific “predisposition“ in relation to its colonization chances?

(5) How far does this explain a species' colonization success or failure?

Due to their biology and distribution leafhoppers are well suited for ecofaunistic studies on different spatial scales as well as for analyses of colonization processes:

- They form diverse assemblages in virtually all terrestrial habitats. On the East Frisian islands they are only absent from the glasswort fields and barren beaches.

- Leafhoppers complete their life cycle within the same habitat. Compared to other groups of arthropods population density is mostly very high. Hence, leafhopper assemblages can be sufficiently surveyed in terms of quantity and quality.

- More than 90% out of a total of 380 species recorded from north western Germany are restricted to distinct habitats. Strong preferences for single host plant species for oviposition or feeding (more than 85% are mono- to oligophagous) is in many cases coupled with a strong preference of a distinct microclimate and, hence, of a distinct habitat (more than 70% are classified stenotopic). In this way, a reliable alignment of habitat data and potential species composition data can be achieved.

- Notwithstanding a certain “homing behaviour“ and a comparatively small range of vagrancy of individuals, the dispersal ability of populations can be regarded as fairly strong: Population waves which occur at times and in places provide a steady proportion of migrating or drifting individuals to render colonization from more or less remote areas within a comparatively short period (e.g. RAATIKAINEN 1972, RAATIKAINEN & VASARAINEN 1973, WALOFF 1973).

Study area

Situated in the southern part of the North Sea off the German mainland the arc of East Frisian islands extends some 90 km along the Wadden Sea (Fig. 1). Some 2000 years ago the dune islands emerged independently from the mainland from a process of sedimentation and subsequent formation of dunes aided by sand-binding plants and since then have been subject to considerable changes in position, size and structure (STREIF 1990). In addition to these 7 "old" islands the investigations were extended to the two smaller islands of Memmert and Mellum which were only formed about a century ago.

On the 7 old islands there are larger villages of several thousand inhabitants each. Increased tourism and related activities has encroached upon the whole natural environment. This appears the more serious, since these islands are part of one of the last pristine landscapes of northern central Europe. Since 1985 the chain of East Frisian islands is largely part of the Niedersächsisches Wattenmeer (Lower Saxon Wadden Sea) National Park.

Due to similar conditions during their history and their linear position along the edge of the Wadden Sea, the 7 old islands developed characteristic sea-land clines of landscape elements and, thus, show a similar basic landscape pattern. In contrast, landscape elements developed to a much lesser degree on the two younger islands. The largely patchy distribution and conspicuous variation of habitats on a small scale leads to an extremely high heterogeneity and a high potential of resources which is unrivalled in most mainland areas.

With respect to size (notwithstanding beach areas and glasswort mud flats) and degree of isolation from the mainland the islands show considerable differences (Tab. 1): Area of the smallest island (Memmert) is merely 7% of the largest (Borkum); the most remote islands are 4 times farther off mainland than the nearest. Habitats and plant life are most diverse on both of the largest islands of Borkum and Norderney, but least rich on the two smallest islands of Memmert and Mellum.

Material and methods

Primarily employed was the method of quantitative sweepnet sampling that proved to be particularly reliable for sampling leafhoppers from herb and tree/shrub strata, respectively (see e.g. EMMRICH 1966, SCHIEMENZ 1969, NIEDRINGHAUS & BRÖRING 1986, 1989; WITSACK 1975; for details on sampling efficacy see NIEDRINGHAUS 1991).

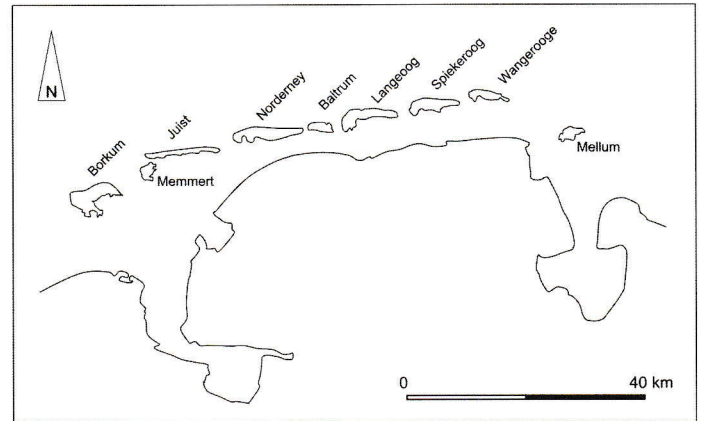


Fig. 1: Geographical position of the East Frisian islands along the southern coast of the North Sea.

	surface area (km ²)	isolation km	landscape-diversity	number of plant species
Borkum	25.6	10.5	2.747	594
Memmert	1.7	13.0	2.560	388
Juist	9.2	8.0	2.713	455
Norderney	17.8	3.0	2.542	342
Baltrum	4.7	4.5	2.617	384
Langeoog	14.3	5.0	2.565	359
Spiekeroog	9.6	6.5	2.571	363
Wangeroog	5.9	6.5	2.000	135
Mellum	3.0	6.0	1.615	200

The quantitative sweepnet samplings were repeatedly conducted in representative sampling sites under suitable weather conditions (not too hot, dry, slight wind) about every four weeks from end of May until mid September of the years 1982 to 1988 (for details see NIEDRINGHAUS 1991). Selection of sampling sites was guided from considering (1) surface area and distribution of habitat classes; (2) achieving as much area coverage as possible with sampling sites most randomly distributed; (3) sufficient representation of heterogeneity within habitat classes; (4) in single cases potential habitats or certain host plants of expected leafhopper species were particularly surveyed.

Tab. 1: Surface area (irrespective of beach areas and glasswort mud flats), degree of isolation (distance from mainland), diversity of landscape elements (number of habitats per 25ha fields) and number of plant species of the islands under investigation (see NIEDRINGHAUS 1991 for further details).

A total of 927 sampling sites (including 264 permanent plots) and 2098 single samplings were analysed. In addition, pitfall traps were used on each island and in all habitats to assess the primarily ground-dwelling (epigeic) species. The material analysed includes 210.000 specimens. Nymphs were usually considered from 3. stage onwards.

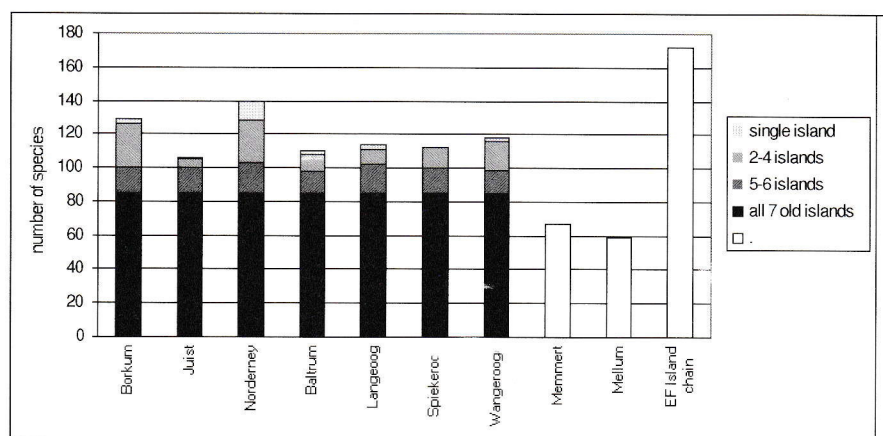
Catch efficiency on the level of individual islands is very high and lies between 89 and 94% (according to trend-analysis/forecasting procedure and jackknife procedure after HELTSHE & FORRESTER 1983).

Results and discussion

The leafhopper fauna of the East Frisian islands

A total of 172 leafhopper species has been assessed from the chain of islands (species list in NIEDRINGHAUS 1991). This amounts to nearly 50% of all leafhopper species known from the north western German lowland (NIEDRINGHAUS & OLTHOFF 1993). The two largest and structurally most diverse islands of Borkum and Norderney are also most diverse in species, harbouring 129 and 139 native species, respectively. Species numbers of the remaining old islands are more or less on a level (Juist 106, Baltrum 110, Langeoog 114, Spiekeroog 112, Wangerooge 118). Irrespective of great similarities in their resource potentials, the islands differ conspicuously in species composition (Fig. 2) and dominance pattern. In the much smaller and – in terms of landscape elements and resources – less diverse islands of Memmert and Mellum 67 species (62 indigenous) and 59 species (53 indg.), respectively, were recorded.

Fig. 2: Species diversity and distributional pattern of leafhoppers of the East Frisian islands.



Some 25% of the species recorded from the islands (nearly 40 species) are less abundant to rare in the remaining parts of north western Germany, but are mostly indigenous and partly common on the islands. Within north western Germany 9 species are exclusively found on the islands or in the adjacent coastal area, namely *Gravestiniella boldi*, *Anacratagallia frisia*, *Aphrodes aestuarinus*, *Psammotettix maritimus*, *Psammotettix sabulicola* in coastal dunes and *Anoscopus limicola*, *Eupteryx artemisiae*, *Macrosteles horvathi*, *Psammotettix putoni* in salt marshes.

The East Frisian islands harbour an extremely rich fauna of more than 10.000 species (BRÖRING et al. 1991), including a high proportion of rare and endangered as well as highly specialized thermophilic species. For terrestrial bugs indigenous to these islands the proportional representation out of the north western German fauna is 46% (BRÖRING 1991), even exceeding 70% for aquatic and semi-aquatic bugs (BRÖRING & NIEDRINGHAUS 1988). Aculeate Hymenoptera and sawflies are represented with 40 %, each (HAESELER 1985, RITZAU 1995), and spiders with 51% (SCHULTZ 1995). However, the question remains, whether and to which extend the species characteristic to the islands become endangered irrespective of the proclamation of the National Park, in that they are banished by organisms being directly (e.g. plantations of various trees and shrubs) or indirectly favoured by human activities. With respect to leafhoppers such species already contribute one third of the present assemblage.

Leafhoppers as indicator organisms of insular dynamics

Even 2000 years after their formation the islands in parts are still subject to a strong dynamic. On the one side, this is due to natural processes (dislocation of sand by the action of seawater and wind, periodic and non-periodic floodings of certain insular parts etc.), but, on the other side, is further occasioned by human activities (punctual and large-scale alterations of the landscape) which greatly increased during the last decades.

This situation is reflected by the present results on the leafhopper fauna from the East Frisian islands. The frequency distributions (species – abundance pattern) of the islands

and biotopes show parallels to those found in species assemblages of unstable and dynamic ecosystems (e.g. BAZZAZ 1975):

The observed distribution patterns in some cases (islands and biotopes) approximate the so-called log-series distribution (more or less linear graph, FISHER, COLBERT & WILLIAMS 1944, Fig. 3a) which is assumed to be largely governed by chance effects. This pattern is found at the beginning of a colonization phase when the successively immigrating species are each exploiting a maximum proportion of a given resource, thus, leaving only "leftovers" for later colonists. Interspecific relationships are supposed to play no role at this stage.

Most islands and biotopes show a distribution pattern intermediate between log-normal distribution (slightly S-shaped graph, cf. PRESTON 1948, 1962, Fig. 3b) and broken stick distribution (distinctly S-shaped graph representing many medium-common species, cf. MACARTHUR 1957, 1960, Fig. 3c). Log-normal distribution patterns are often found in areas where succession has reached a more or less mature state, but which are still subject to moderate dynamic processes. A broken-stick distribution appears where competition between the species of an assemblage prevails over other more or less independent abiotic factors and resource partitioning and niche separation have advanced.

In most cases the distribution patterns appear "torn", i.e. there are more or less irregular deviations from the theoretically expected pattern (particularly regarding the medium-common species). These indicate conspicuous qualitative and especially quantitative fluctuations within the species assemblages. Permanent changes in the availability of resources (caused by natural and human impact) impede the formation of distinct and stable species assemblages.

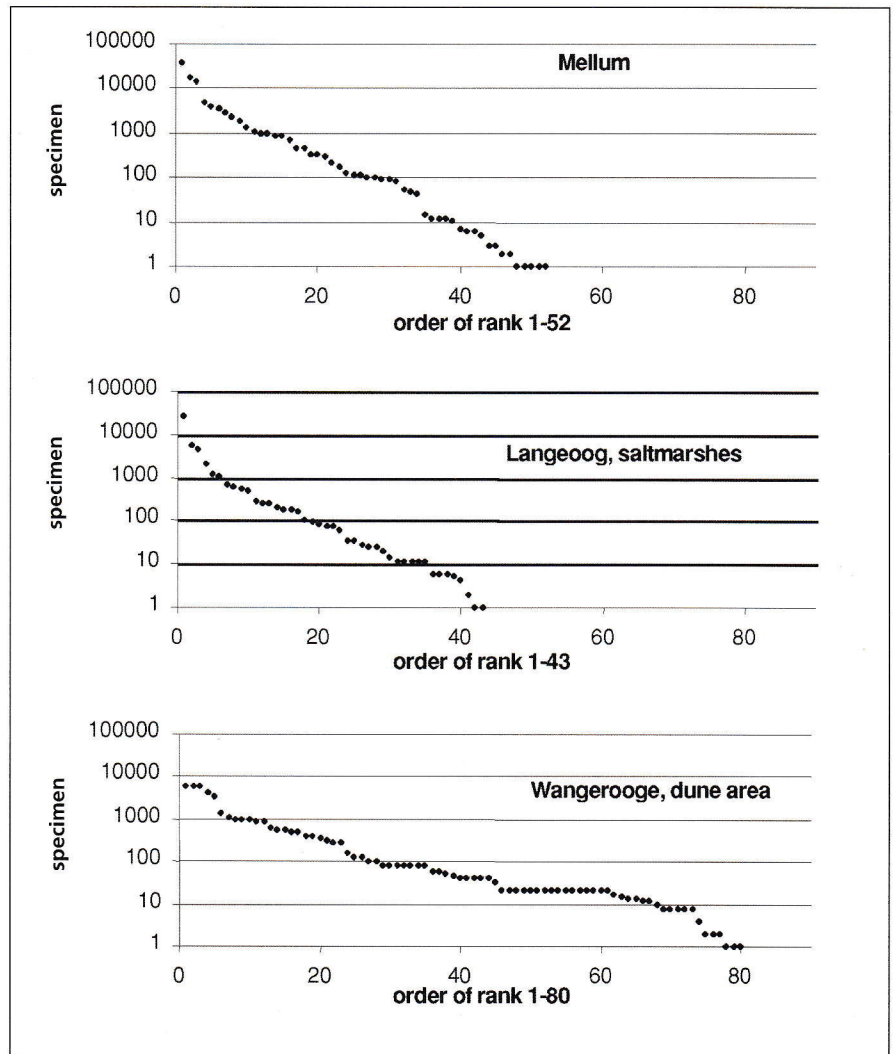
Leafhoppers from the perspective of insular biogeography

Colonization success of the leafhoppers from the East Frisian islands

Since – unlike the North Frisian "Geestcore" islands – the East Frisian dune islands were never connected to the mainland, all

colonizing plant and animal species had to immigrate from outside. With distances of 1 to 11 kilometres off mainland and between each other their degree of isolation is fairly low. Although most investigations on insular biogeography focus on the bird life of islands of much greater isolation (of up to several thousand kilometres), the available analyses of arthropod assemblages usually pertain to

Fig. 3a-c: Distribution patterns of the leafhopper assemblage (represented from most common to the rarest species).



islands as little isolated as those in the present study (e.g. AS 1984, NIEMELÄ et al. 1985, BOOMSMA et al. 1987, NILSSON et al. 1988). In some cases distances to the source areas amounted to a few to some hundred meters, only (e.g. WILSON & SIMBERLOFF 1969, REY 1981).

Leafhoppers, as a comparatively vagrant group of insects, are not impeded to bridge distances of a few kilometres (c.f. e.g. STEARNS & MC CREARY 1938, HOLZAPFEL & PERKINS

1969, WOLF et al. 1986), at least within a longer colonization period. It should, therefore, not surprise that no relation could be established between numbers of species and degree of isolation (Fig. 4a), nor between colonization success and dispersal ability (Fig. 4b).

Naturally, not all of the 380 leafhopper species known from the north western German lowland are able to establish themselves

tion rates found on the younger islands of Memmert and Mellum (67 and 70%) are in first line attributable to a high proportion of eurytopic species and species being common within the recruitment area which, therefore, experience higher colonization chances. Whether such colonization rates are to be considered high or low and which conclusions to draw cannot be settled here in want of further studies on additional animals groups.

Fig. 4:
(a) Relation between numbers of species and degree of isolation,
(b) relation between colonization success and dispersal ability.

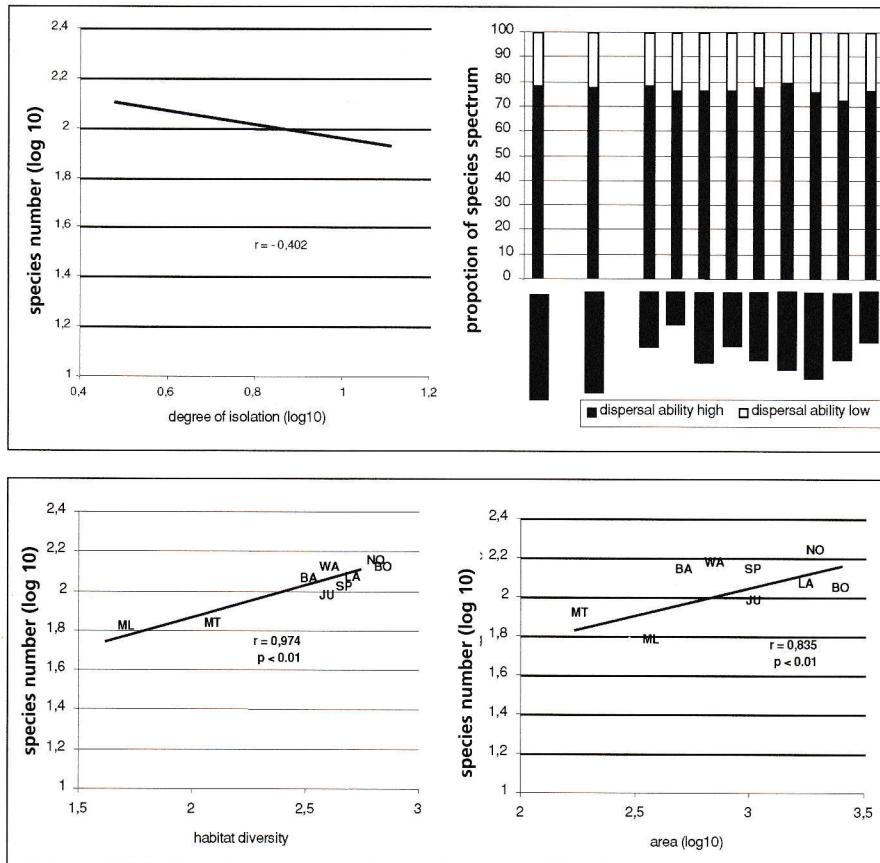


Fig. 5:
(a) Relation between species number and island habitat diversity (a) and island area (b).

on the chain of islands. Considered as potential colonists are only those species from the recruitment area (i.e. roughly the mainland region within a radius of some 150 km from the islands; see NIEDRINGHAUS 1991 for details) the resource requirements of which are sufficiently met on the islands. Given this, 236 species are regarded as potential colonists for the chain of islands as a whole (between 212 and 236 spp. each for the old island, 92 and 76 spp., respectively, for the young islands of Memmert und Mellum). Hence, the “colonization rate“ is about 71%, in other words, 29% of the potential colonists currently failed to establish themselves. For the old islands colonization rates range between 49 % (Juist) and 59 % (Norderney). The higher coloniza-

Factors affecting the colonization success

Leafhopper species numbers of the East Frisian islands are more closely related to their habitat diversity ($R = 0,974$, $p < 0.01$) than size ($R = 0,835$, $p < 0.01$; Fig. 5a,b). Hence, the present data do better fit the “habitat-diversity hypothesis“ (WILLIAMS 1964: species numbers of isolated areas dependent on its diversity of landscape elements) than the “area-per-se-hypothesis“ (MACARTHUR & WILSON 1963, 1967: species numbers of isolated areas dependent on its size).

Conversely, species numbers of bugs from the East Frisian islands are more closely related to island size than diversity of landscape elements (BRÖRING 1991): In this group island size explains more than 72% of the variances of deviation (partial correlation with diversity maintained constant), but merely 23% in leafhoppers (NIEDRINGHAUS 1991:86). Diversity of landscape elements explains only 56% in bugs, but 82% in leafhoppers. These findings may be explained by the following argument:

1. Compared to bugs leafhoppers generally show higher population densities and reproductive rates and presumably also a greater vagrancy particularly as to larger distances. This ultimately renders a faster and more “complete“ colonization of potential habitats.

2. There are comparatively numerous members of leafhoppers exerting minimal areas of a few square meters, only. Since the potential habitats are usually much larger on the islands, insufficient habitat size would not play a role as a prerequisite for a successful colonization in such cases.

3. On all old islands the potential of resources increased through human activities (e.g. shrub and tree plantations) within the last decades. In this way, species spectra of

leafhoppers increased considerably on the islands (by some 50 to 60% each). These new habitats being independent of island size are fast colonized by leafhoppers (see point 1.).

While according to the area-per-se approach exclusively quantitative aspects have an effect (island area and species numbers of colonists), the importance of qualitative aspects (number and specificity of potential habitats, species numbers of colonists and composition of species assemblies) is stressed by the habitat-diversity approach. Thus, the analysis of colonization success of the species under study demands the evaluation of those characteristics which may affect the colonization process, particularly with respect to the questions: "Why are certain species absent from the islands?" and "Why are certain colonist species more successful than others?"

For the group of leafhoppers the following characteristics were considered as potentially affecting the colonization chances:

1. dispersal ability;
2. preference for special groups of host plants;
3. feeding specificity in terms of host plant taxa;
4. hibernating stage and number of generations per season;
5. body size;
6. habitat preference;
7. preference for particular stages of the landscape development on the island (potential duration of the colonization period);
8. degree of niche overlap;
9. abundance in the recruitment area.

Whether these characteristics are strictly causal or merely "observed effects" being linked to other characteristics cannot be decided at present.

Five characteristics (2, 6, 7, 8, 9) are more or less related to the colonization success on the islands (Tab. 2). All other components seem negligible in this respect.

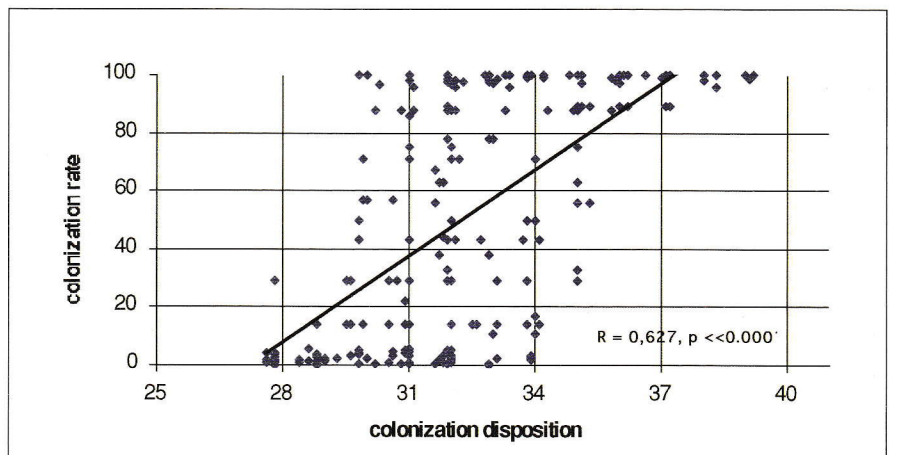
Corresponding to its specific combination of characteristics each potential colonist species appears more or less "qualified" for successfully colonizing an islands. Each species is distinguished by a certain "disposition" which raises or reduces its colonization chances. In order to facilitate further analysis, for each potential colonist a specific "colonization disposition" (CD) value has been calculated for each potential colonist by summing up the various factor values (for details see NIEDRINGHAUS 1991).

11 species (5%) out of the total of 235 species regarded as potential colonists (see above)

are characterized by very low disposition values (CD 25 to < 28; very small colonization chances), 56 species (24%) by low (CD 28 to < 31), 46 species (20%) by high (CD 34 to < 37) and 13 species (6%) by very high (CD ≥ 37) disposition values. 109 species are indifferent in this respect, i.e. their colonization chances appear to be neither increased nor decreased (Fig. 6).

Tab. 2:
Relation between colonization success and various factors (deviations of characteristics-fractionated rates of success from mean rates).

2. preference for special groups of host plants	grasses 8 ± 3	sedges/rushes -1 ± 9	herbs 3 ± 5	woody plants -10 ± 5
6. degree of habitat specialization	highly eurytopic 29 ± 7	eurytopic 3 ± 2	stenotopic -23 ± 6	highly stenotopic -8 ± 5
7. potential length of colonization period	very long (ca. 2000 years) 27 ± 5	long 11 ± 2	short -9 ± 3	very short (ca. 100 years) -31 ± 5
8. degree of niche overlap	high -11 ± 4	medium -1 ± 9	low 11 ± 9	
9. abundance in the recruitment area	very abundant 35 ± 14	abundant 10 ± 9	rare -12 ± 6	very rare -10 ± 10



The relation between colonization success (proportion of successfully colonized versus available islands) and colonization disposition is highly significant, although its explanatory value is not particular high because of the many indifferent species ($R = 0,627$, $p << 0,0001$). After deleting these indifferent species this relation increases to $R = 0,805$, $p << 0,0001$. For the 127 potential colonist species showing a determined disposition the expected and observed colonization success match to 90%. Nevertheless, 14 species (10%) do not meet this expectation. These include potential colonists with low disposition values experiencing a colonization success higher than expected, on the one side, and colonists with high disposition values yielding a low colonization success or none at all, on the

Fig. 6:
Relation between colonization „disposition“ and colonization success.

other. Whether these findings are indicative of chance phenomena or further unknown factors remains to be settled.

In contrast to the approaches and models of insular biogeography relying on purely quantitative parameters (numbers of species of isolated areas as a variable to be explained) the present study aims at the individual species and their biological-ecological characteristics as a starting point of reasoning. The focus lies on qualitative aspects (the specific combination of species as a variable to be explained) and, thus, on the uniqueness of the studied species assemblage.

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Zusammenfassung

Von 1982-1988 wurden auf den im Wattenmeer der südlichen Nordsee gelegenen 7 alten Ostfriesischen Inseln Borkum, Juist, Norderney, Baltrum, Langeoog, Spiekeroog und Wangerooge sowie auf den beiden jungen Inseln Memmert und Mellum inselbiogeographische Untersuchungen zur Zikadenfauna (Hemiptera, Auchenorrhyncha) durchgeführt.

Auf der Inselkette wurden insgesamt 172 Arten nachgewiesen. Die Artenzahlen der alten Inseln liegen annähernd auf gleichem Niveau (110-139 Arten). Die Artenzusammensetzungen zeigen trotz starker Ähnlichkeiten der Ressourcenpotentiale der Inseln allerdings erhebliche Unterschiede. Die Muster der Häufigkeitsverteilungen zeigen in vielen Fällen ausgeprägte Parallelen zu Artenzusammensetzungen dynamischer und nicht ausgeprägter Landschaften.

Der Isolationsgrad der Inseln ist zu gering, als daß der Kolonisationserfolg der Zikaden davon beeinflußt wird: Weder zwischen Artenzahl und Isolationsgrad noch zwischen Kolonisationserfolg und Dispersionsfähigkeit ergeben sich Korrelationen. Die Zikaden-Artenzahlen der Ostfriesischen Inselkette lassen sich besser durch die Variablen der

landschaftlichen Diversität als durch die der Flächengröße erklären. Die Daten zur Zikadenfauna dieser Inseln sind insofern eher mit der "habitat-diversity-Hypothese" als mit der "area-per-se-Hypothese" in Einklang zu bringen. Die Gründe dafür sind sowohl in spezifischen Eigenheiten der Zikaden zu finden (z.T. starke Lebensraum-Spezialisierung und damit zusammenhängend effiziente und schnelle Besiedlung potentieller Habitats, z.T. sehr geringe Minimallebensräume) als auch in spezifischen Eigenheiten der Inseln (permanente Dynamik hinsichtlich der landschaftlichen Entwicklung, Entkopplung von Inselgröße und Anzahl potentieller Habitats durch künstliche Diversifizierungen der Inseln).

Es besteht ein Zusammenhang zwischen dem Kolonisationserfolg und bestimmten Merkmalen der potentiellen Kolonisten; entscheidende Komponenten dabei sind: der Spezialisierungsgrad hinsichtlich Lebensraum, die Nahrungspräferenz für bestimmte Pflanzengruppen, die Präferenz für bestimmte landschaftliche Entwicklungsstufen auf den Inseln, die Einnischungsfähigkeit gegenüber Konkurrenten, die Häufigkeit im Rekrutierungsareal. Weitere mögliche Komponenten wie Dispersionsfähigkeit, Grad der Nahrungsspezialisierung, Überwinterung, Generationszyklus oder Körpergröße spielen hinsichtlich der Kolonisationschancen keine nennenswerte Rolle.

Jeder einzelne potentielle Kolonist verfügt aufgrund seiner spezifischen Merkmalskombination über eine bestimmte „Disposition“, gemäß der seine Kolonisationschancen steigen oder fallen. Die Quantifizierung dieser „Kolonisationsdisposition“ ergibt: 3% der potentiellen Kolonisten zeichnen sich durch sehr niedrige Dispositionswerte (stark verminderte Kolonisationschancen), 22% durch geringe, 21% durch hohe und 9% durch sehr hohe Dispositionswerte aus. Fast die Hälfte aller potentiellen Kolonisten (46%) erweist sich als m.o.w. neutral, so daß bei ihnen weder von erhöhten noch von verminderten Kolonisationschancen auszugehen ist. Ist die Kolonisationsdisposition jedoch gerichtet, so werden - wie die Prüfung der tatsächlichen Erfolgswerte ergibt - für 90% der entsprechenden potentiellen Kolonisten die Erwartungen hinsichtlich ihres Kolonisationserfolges bzw. Mißerfolges auf der Inselkette erfüllt.

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