ECOLOGICAL INDICATORS

The definition of a new plant diversity index "H'_{dune}" for assessing human damage on coastal dunes—Derived from the Shannon index of entropy H'

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Abstract

The presented paper shows that the common usage of H' is not an appropriate index of plant diversity for studying disturbance in plant communities. H' is strongly dependent on evenness, whereas species richness and species density are not adequately incorporated. Therefore, the common usage of H' is only a measure for relative diversity in respect to the maximum possible diversity for each community. Furthermore, using the abundance of species relative to the total abundance of all species will result in the loss of information on species density (plant cover) when H' is calculated and comparisons between disturbed and undisturbed communities become difficult. Instead it could be shown that the newly introduced index H'_{dune}, which uses the species abundance (as coverage percentage) relative to the constant sampling area for calculation, will more clearly detect changes in species richness and composition. Sample size (plot size) is always constant and information on species density (coverage) is also incorporated in the index. H'_{dune} is used to compare different coastal dunes along the southern Baltic Sea coast of Germany and Poland which differ in the degree of disturbance from recreational activities. The two main changes observed were damages because of trampling and a change in species composition, because of increasing nutrient levels. Two methods to detect different types and levels of anthropogenic disturbance and stress from recreational activities on coastal dunes are presented.
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1. Introduction

The Shannon Index of entropy H' is often used in ecological studies (Mouillot et al., 2005; Townsend et al., 2002; Patil and Taillie, 1982). Since it is regarded as an appropriate measure for diversity the present study tests its applicability for detecting anthropogenic changes in plant diversity on coastal dunes along the southern coast of the Baltic Sea (Fig. 1). Following the discussion of H' an adapted index H'_{dune} is presented which incorporates the parameter species density (plant

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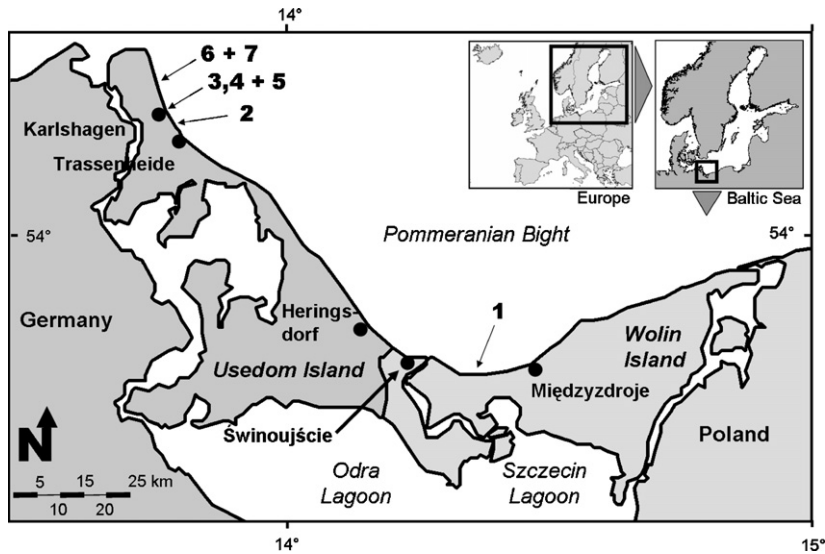(R. Grunewald).

Fig. 1. Pommeranian Bight and study sites (BM = intensive beach management/cleaning) (1 = Wolin, undisturbed; 2 = between Trassenheide and Karlshagen, undisturbed (no BM); 3 = Karlshagen, Camping (BM); 4 = Karlshagen, northern resort (BM); 5 = near between Karlshagen and site 6 (no BM); 6 = Parking, north of Karlshagen (BM); 7 = north of site 6 (no BM, only few visitors)).

cover relative to the plot-size) into the diversity calculations (Fig. 2).

This paper is not aimed at giving a thorough review of literature on diversity indices, since several authors, e.g., Magurran (1988), Peet (1974) or Pielou (1966), already give good introductions into measuring diversity; nevertheless, it is necessary to state the two major components of diversity: Species richness and relative abundance of species. How many species are there in a given set (of individuals, biomass, plant cover per area) and how abundant are they (or biomass, plant cover). Some indices are aimed at either measuring just species richness (e.g. Margalef) other measure only evenness (how evenly are the individuals distributed among the different species). A different type of indices tries to incorporate both

$$H' = - \Sigma \, p_i * \ln(p_i)$$

Shannon and Weaver (1949)

p_i = coverage percentage of the ith species (relative to the summed total plant coverage, see note below); the choice of logarithm used is not defined (see also note below)

$$H'_{dune} = - \Sigma \, p_{i\text{-}dune} * \ln(p_{i\text{-}dune})$$

$p_{i\text{-}dune}$ = coverage percentage of the ith species (relative to the plot size)

Note:

According to literature (other than Shannon and Weaver 1949) on calculating H', p_i is "defined" as:

$$(p_{i\text{-}dune}) * (\Sigma p_{i\text{-}dune})^{-1}$$

$$H'_{dune\text{-}max} = -s * [((\Sigma p_{i\text{-}dune})/s) * \ln((\Sigma p_{i\text{-}dune})/s)]$$

$(\Sigma p_{i\text{-}dune})/s$ = average coverage percentage

$$H'_{max} = \ln s$$

s = number of species

$$E_{dune} = H'_{dune}/H'_{dune\text{-}max}$$

E = Evenness

$$N = H'_{dune} \text{ (without alien species)}/H'_{dune}$$

N = degree of natural diversity

Fig. 2. The definition of H' and H'_{dune} (including other parameters calculated using H' or H'_{dune}).

components of diversity into a single value, e.g. Hurlberts PIE-index, Simpson's diversity index or the widespread index H' by Shannon (Shannon and Weaver, 1949). Some are weighted towards the more dominant species (Simpson) others give rare species more weight in the index (H', Mouillot and Leprêtre, 1999). However, according to literature, most indices – including H' – make use of the relative abundance of each species in respect to the total number of individuals (biomass, cover) sampled. Thus 2 communities with 5 species each would not differ in diversity if the first community would have 50 individuals evenly distributed among the 5 species and only 5 individuals for the second (possibly disturbed) community (each species is consequently represented by only one individual). Additionally, a single species 'community' does not differ from a sample without any species. Nevertheless, these communities are very different.

Therefore, it is necessary to take a closer look at H' and how it was developed. Shannon (Shannon and Weaver, 1949) described H' as an information index or an index of entropy, which was initially used to analyze and measure information. How much information is stored in a given set of data (amount of information, p. 8) and how much could potentially be stored (capacity, p. 8). Much is said about "information content", "capacity", "probability" and "entropy". Nothing is said about ecological questions such as "species density", "interspecies competition", "biomass" or even "diversity".

Translating Shannon's approach on information content and degree of entropy into the ecological meaning of diversity, the paper will try to show that the present usage of H' does not take species density (i.e. species presence/absence or abundance in respect to habitat) into account and therefore fails to detect major changes in dune habitats due to disturbance. The authors believe that species density is a major parameter for studying community structure and diversity. This is especially true for the study of disturbance and extreme habitats like dunes.

The harsh dunal environment with strong sun radiation, poor sandy soils, minimal water supply, salt stress and mechanical stress from moving sand is the dominant factor leading to the presence of highly adapted specialized species which can tolerate these conditions (Hesp, 1991). Competition for space and/or light (inter species competition) is not dominant on many dunes, but salt spray, mechanical stress (from moving sand), nutrient availability and water supply are key factors for plant life (Maun, 2004; Kooijman and Besse, 2002; Packham and Willis, 1997; Ellenberg, 1996; Hesp, 1991). Only on older dunes, where salt spray, nutrients and water are no longer exclusive limiting factors, competition for space as well as light will take place and will also affect species richness (Tilman's "equilibrium model of plant resource limitation" in Hobohm, 2000; Tilman et al., 2001).

The most obvious short time dynamics in beach and dune systems are caused by heavy storm surges, but constantly blowing winds cause long time changes and most of the sand accumulation; therefore, aeolian processes are most important for dune development complemented by effects from dune vegetation and water (Hesp, 1991). On prograding coastlines along the southern Baltic Sea coast new dune habitat is constantly being formed by the continuous sand supply. Plants break the wind speed causing sand mobilized by the wind to settle and to build up small primary dunes and start primary succession on the upper beach (Grime, 2002; Hesp, 1991). Over time more sand is being accumulated and new species, typical for secondary dunes start to appear (e.g. Hesp, 1991; Ellenberg, 1996). Different stages of primary succession will appear along a beach land gradient and plant and soil succession continues: $CaCO_3$ is being leached out of the dunes, pH decreases, humus starts to accumulate, and tertiary dunes develop. A typical natural zonation along the southern Baltic Sea coast from the upper beach towards the land will lead from young successional stages of vegetation with low species numbers to more mature stages with higher species numbers and only on brown dunes—after inter species competition (competition for limited resources) becomes the dominant factor for species presence or absence—species numbers mostly decline (Hesp, 1991). Such effects of species competition and diversity were also found by Goldberg and Estabrook (1998), who studied the competitive exclusion of species in communities characterized by high numbers of individuals per unit area.

Fig. 3 shows one typical and one unchanged transect through coastal dunes indicating different beach and dune zones along the southern Baltic Sea
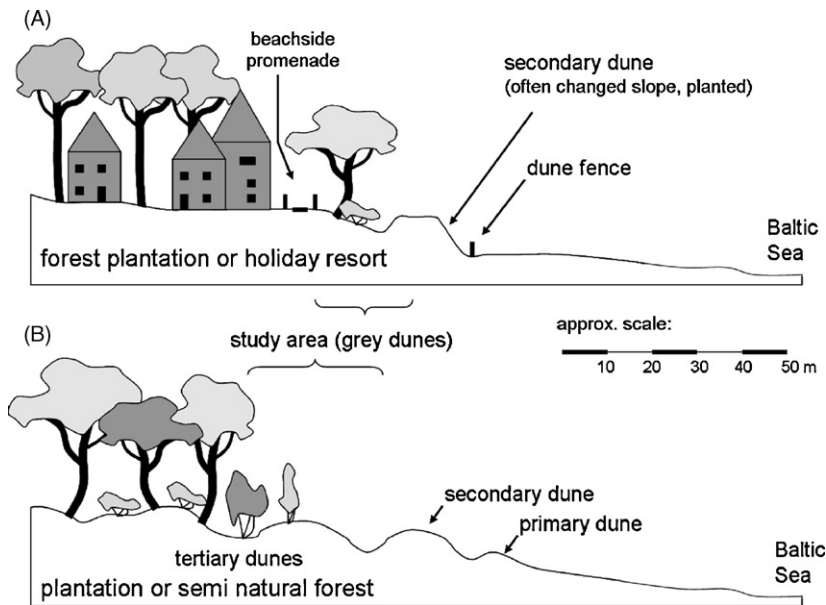
Fig. 3. Two transects through coastal dunes along the southern Baltic Sea coast. (A) Transect changed by recreational activities—now typical for large parts of the dune coasts along the southern Baltic Sea Coast in Germany. (B) Unchanged natural transect.

coast according to the definition by v. Nordheim and Boedeker (1998) in the Red List of Biotopes and Biotope Complexes of the Baltic Sea the Belt Sea and Kattegat. Besides coastal defense measures and building activities, two main anthropogenic impacts on southern Baltic Sea dunes are frequently discussed in literature (e.g. Piotrowska and Gros, 1998; Knapp, 1996; Isermann, 1995; Jeschke, 1985).

- Mechanical damages through trampling will directly damage plants and the vegetation cover is reduced or even destroyed (sand remobilization) which will lead to secondary succession once the disturbance has stopped (Grime, 2002).
- Eutrophication as a result of faecal deposits from tourists or gardening activities in the vicinity of holiday resorts will dampen the extreme habitat conditions on the dunes and untypical ruderal plants have a chance to establish themselves—changing the species composition. Grime (2002) suggests that'' fluctuations in resource availability (e.g. nutrients) are the key factor controlling plant community invasibility.''

The aim of the study was to analyze the extent of anthropogenic disturbance along different parts of the coast and the hypothesis was that 'natural diversity' can be used as an indicator. For this study disturbance was defined as any human impact (related to recreational activities) which will result in changes in species diversity and/or community structure, which is a broader definition than the one by Grime (2002), but close or the same to the one used by Pickett and White (1985). Since it is known, that low levels of (human) disturbance (intermediate disturbance hypothesis, Connell, 1975) may result in a rise in diversity, the term 'natural diversity' was used. Hill et al. (2002) showed that increasing levels of anthropogenic impact correlate with increasing numbers of alien species. Therefore, species which are either alien species to Germany or Poland or alien to the unchanged (natural) dune habitat were used as additional indicators for disturbance (human influence, hemeroby, Kowarik, 1999).

After testing the applicability of H' for field data from Wolin Island and Usedom Island (Poland and Germany), different adaptations of this index were developed. As a result it could be shown that H' is not an adequate measure for anthropogenic disturbance in coastal habitats, especially dunes. In the end an alternative way of calculating H' was developed which is indicated by adding the suffix ''dune''. The

applicability of this newly introduced diversity measure for other types of habitats must still be proven in forthcoming research.

2. Material and methods

2.1. Study sites and sampling methods

2.1.1. Study area

The presented data was gathered from 2002 to 2004 on the German part of the Island of Usedom/ Uznam and on the Polish Island of Wolin (Fig. 1). The temperate climatic conditions are very similar (yearly mean approx. 7.5 °C; yearly precipitation: 575 mm, Reinhard, 1951, 1962; Müller, 2004) and coastal exposition differ only little between the sites (Fig. 1). Westerly winds prevail during most of the year, but storm surges with peak wind speeds mostly come from northeasterly directions from November to February (Hurtig, 1957). The type of sand building up the dunes is also very similar in mineral composition as well as grain size (Isermann, 2001) and all sites are along potentially prograding coastlines with a similar zonation (Fig. 3). All study sites should therefore share a similar potential for dune vegetation.

Usedom and Wolin are located in the Polish–German trans-border-region and tourism is one of the few thriving industries (Seidel, 2001). Poland joined the European Union in 2004 and growing numbers of visitors are expected in the future, whereas tourist numbers and tourist infrastructure are already very high in Germany. Since large stretches along the Wolin coast (Poland) are only accessible by foot or bicycle, these areas remain in a fairly undisturbed ecological state (Grunewald and Łabuz, 2004) and coastal recreation in northwestern Poland is concentrated mostly around the holiday resort of Międzyzdroje and the city of Świnoujście. Fig. 1 shows the seven different study sites which were chosen because of expected and observed differences in recreational activities. Sites 1 (on the central part of Wolin between Międzyzdroje and Świnoujście) and 2 (a remote beach and dune area between the holiday resorts of Karlshagen and Trassenheide) both represent areas which are only accessible by foot or bicycle (over 2 km from the nearest parking area or hotel). Site 3 is adjacent to a large campground south of Karlshagen

and mostly campers use the beach. Intensive beach cleaning operations are carried out at site 3 and at site 4, which is in Karlshagen. This site is used by many holiday makers and daytime tourists who use the nearby parking areas. Site 5 is just north of the resort and no intensive beach cleaning is carried out. This site is mostly visited by holiday makers from the resort and some visitors from parking areas, but numbers are lower than in the resort itself or at site 6, which is adjacent to a large parking lot. Many day tourists and overnight campers (also illegal camping in the dunes) use the beach and intensive beach cleaning operations are carried out. About 1 km north of site 6 is the remote site 7. Only few people walk the distance from the parking lot and intensive beach cleaning is not carried out. Sites 1 and 3 were only used for studying tertiary dunes and sites 5 and 7 were only used for studying primary dunes.

In addition to the sites mentioned above, several other dunes along the islands of Usedom and Wolin were also studied and altogether data from 429 plots (249 plots from tertiary and 180 from primary and secondary dunes) are used for some statistical analysis of the calculated diversity parameters.

2.1.2. Sampling methods

The method by Braun-Blanquet (1964) and Barkman et al. (1964) was used to document plant species presence and coverage. The minimum area was determined according to Dierschke (1994) and a constant plot-size of 16 m² was chosen for tertiary dunes (grey dunes) and 4 m² for primary and secondary dunes.[1] The analysis of tertiary dunes was separated from the study of primary and secondary dunes. According to Braun-Blanquet (1964) only homogenous plots were studied so that any effects from different habitat conditions within one plot could be eliminated (habitat diversity influences species diversity). The method of documenting each species and its coverage can be seen as a "non-destructive estimate of biomass" (Tilman et al., 2001) and is a common procedure to document plant communities and study diversity patterns. Since mosses and lichens are both on the same trophic level

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[1] Isermann (1997) found similar values: even 4–8 m² may be sufficient for some plant communities on tertiary dunes. For secondary dunes it is important to have plots parallel to the coastline (even 1 m² may then be a sufficient sample size).

as vascular plants and make up a fair amount of plant diversity on dunes, pedogenic lichens and mosses were included in the study.

As stated above, the analysis of primary and secondary dunes was separated from the analysis of tertiary dunes. The methods for plot selection also differ between tertiary (older dunes) and secondary and primary dunes (younger dunes), hence both methods are described separately.

2.1.3. Primary and secondary dunes

The vegetation of primary and secondary dunes was sampled on Usedom Island (in Germany, Fig. 1) at the sites 2, 4, 5, 6 and 7. Between these sites visitor numbers as well as the level of beach cleaning operations and beach control (e.g. life guards) differ a lot.

Along the German Baltic Sea coast most secondary dunes are protected by a small fence at the base of the secondary dune and no trespassing is allowed; since these fences are always positioned in the same distance from the dune (between the secondary dune and the zone where primary dunes may form), it can be used as a reference line (Figs. 3 and 4). These fences are constructed from wooden poles (4 m apart, 80 cm high) and a single wire so that any effect on sand accumulation initiated by the fence should be minimal. Since it is always positioned at the base of the secondary dune (where sand accumulates to form new primary dunes) the fence was used to ensure that the same dune zones are compared with each other. Even though the fence is largely respected, people do not hesitate to cross the fence and defecate on the dunes. The common effect observed was that along coasts with some recreational activities the dunes are damaged in a mosaic pattern. Small pockets of bare sand (from trampling and sunbathing tourists) alternate with areas covered with dense vegetation. The objective was to study this pattern and use the differences between sites as well as between the upper and lower plots as indicators for recreational activities. Therefore, at each site a 30 m long representative stretch of the fence, typical for this part of the beach, was marked with measuring tape and every 2 m plots of 2 m × 2 m (on each side of the measuring tape/ fence) were documented. The resulting 30 plots (15 behind, 15 in front of the fence) covered the variability of the vegetation within this site. Any larger plot-size

Fig. 4. View of the primary/secondary dunes and beach north of Karlshagen (April 2003). At the base of the secondary dunes, the small dune fence protecting the secondary dunes is visible. (1) The area immediately below the dune fence is the most popular spot for sunbathers. (2) Only in some distance from the dune fence damage from trampling is low and primary dune vegetation can develop (photo taken in April). (3) Intensive mechanical beach cleaning will remove debris washed ashore (including diasporas, rhizome). All plants are destroyed and small primary dunes are leveled (right foreground). (4) In the area of intensive beach cleaning, sand is blow across the bare beach and partly accumulates on the secondary dunes.

would not adequately reflect the mosaic vegetation pattern on the beach.

2.1.4. Tertiary dunes

The vegetation of tertiary dunes was sampled on the German part of Usedom Island as well as on Wolin Island (Poland, Fig. 1). Site 1 on Wolin Island was chosen as an example for tertiary dunes with almost unchanged typical dune vegetation (Grunewald and Łabuz, 2004). The other sites for tertiary dunes were chosen, because the adjoining beaches represent different levels of recreational use, which should also lead to different levels of impact on the dunes. Nevertheless the impact on dunes was not directly measured, but estimated using the parameters accessibility, control of the beach (e.g. life guards), and the number of visitors on the beach (not on the dunes).

Similar to the situation on primary and secondary dunes, heavy mechanical damages to the vegetation through trampling are clearly visible on tertiary dunes. They often alternate on a small scale with almost unaffected areas. Because of plant succession along the beach-land gradient (Isermann, 1997; Hesp, 1991)

the obvious method would be to document plots from each stage of dunal plant succession and compare each dunal zone from each study site with the same dunal zone from the other sites. However, the dunes and each dunal zone do not have exactly the same width. The identification of each zone is difficult, because the plant community growing or the soil condition in this area may already be the result of human disturbance: mechanical damages may be interpreted as a setback in succession and the resulting secondary succession may lead to vegetation which is still a typical dune community—only growing further inland (high naturalness, high hemeroby, Kowarik, 1999). The human induced rise in nutrients may result in an accelerated succession, the resulting vegetation again may be a typical dune community—only growing closer to the beach than normal (high naturalness, high hemeroby). Therefore, it was decided not to compare exactly the same dune zone from different sites with each other.

Instead the following protocol to choose the individual plots was used: Three transects were documented at each study site. Each transect started on the youngest grey dunes with a 16 m^2 plot and the last plot was made on the oldest non-forested dunes. One transect covered the areas exhibiting the highest degree of damage (e.g. large illegal footpaths, fire sites), one with intermediate damage, and one with the lowest level of damage. The study mainly focused on the open dunes, but single bushes or trees were incorporated into the study. Very steep southern slopes with naturally occurring erosion (strong sun radiation in combination with high surface temperatures and lack of water, Grunewald and Łabuz, 2004; Hesp, 1991) were also excluded from the investigation. The number of plots per study site may vary, because of the different widths of the dunes at each study site. However, three complete transects from young grey dunes to the older non-forested dunes were documented and grouped for each of the five sites. Since all sites should share the same potential for phyto-diversity, this method ensured that the variability of the different dune zones was documented and problems identifying certain dune zones did not occur. It also ensured that the variability of the different levels of human disturbance through trampling was reflected in the different plots.

2.2. Calculations

The following parameters were calculated from the gathered field data. Calculation of the diversity index H' and the adapted index H'_{dune} (Fig. 2) was done in order to compare their sensitivity for changes on dunes. Since evenness is often used as a parameter for community structure (independent of species richness), the calculation using H'_{dune} is also presented. For its calculation it is necessary to first calculate the average species coverage in each community and then the maximum value for H'_{dune} for this combination of total cover and number of species ($H'_{dune-max}$). H'_{dune} will reach a maximum value ($H'_{dune-max}$), if all species are equally abundant. Similar to the calculation of E (using H'), E_{dune} is the ratio between H'_{dune} and $H'_{dune-max}$.

Besides overall diversity, qualitative changes in species composition were studied as well. It was expected that the number of ubiquist or ruderal species will increase as a result of rising nutrient levels on tertiary dunes in areas with a high level of tourism. Neighbouring effects from nearby public parks and private gardens in the vicinity of holyday resorts were also expected to influence species diversity (species pool hypothesis, Pärtel et al., 1996) so that a rise in overall diversity may very well be a result of increasing levels of human influence. The degree of natural diversity (N) was calculated by classifying the present species into typical native dune species and untypical dune species alien to the extreme dune habitat (including truly alien species). The diversity index H'_{dune} was then calculated twice: with all present species and without the species alien to the dunes (the later can be seen as a measure of natural diversity). The ratio between the two can now be seen as the degree of natural diversity. Species which are untypical for undisturbed dunes cannot cope with the extreme habitat conditions—once they appear, they indicate change. Increasing nutrient levels are a key factor for the invasibility of habitats for ruderal species (Grime, 2002). Similar to the calculation of evenness, the ratio will be independent of species diversity and only a maximum value of one can be reached (if no species are excluded = complete natural diversity). The following species were excluded from calculating natural diversity: *Acer platanoides*, *Acer pseudoplatanus*, *Aira praecox*, *Artemisia vulgaris*, *Campylopos introflexus*, *Conyza canadensis*, *Crataegus* spec.*, *Elaeagnus angustifolia*, *Elaeagnus commutata*,

Prunus serotina, *Rosa rugosa*, *Sambucus nigra*, *Sedum sempervivum*, *Solidago virgaurea*, *Symphoricarpos albus*, and *Tortula ruraliformis*. Most of the chosen species are also alien species to Poland or Germany, but also some native species alien to the dunal habitat were excluded. The classification was based on habitat requirements taken from literature (Ellenberg et al., 1992; Haeupler and Muer, 2000). The classification of the moss *Tortula ruraliformis* is based on personal experience as well as a on a study by Berg et al. (1995).

In order to compare the different diversity parameters and the weight in calculating the diversity indices (H', H'_{dune}, E, E_{dune}) correlation methods were applied. For the discrimination of dune sites, it was expected that damaged sites should significantly differ from unchanged dunes. Therefore, data was also analysed using ANOVA like Kruskal–Wallis One-way Analysis of Variance on Ranks (including all pair wise multiple comparison procedures, $p < 0.05$).

3. Results and discussion

3.1. Application of H' on dune vegetation

Table 1 summarizes the results of five selected plots from primary dunes. Species numbers on primary and

secondary dunes are quite low and all species are named with their respective coverage (%). Even though large differences in total and individual coverage exist between the plots, the small differences in evenness values result in almost similar H' values. Only one plot (4) shows a relative low value for H', which is caused by the dominance of *Petasites spurius*, reflected in a low evenness. This community also has the highest total plant cover.

The plots shown in Table 1 differ with respect to anthropogenic impact. Whereas plots 2 and 4 (both at site 2) showed no obvious signs of anthropogenic impact, visible signs of anthropogenic induced mechanical stress (footprints, garbage) were observed at plots 1, 3 and 5 (all at site 4). Trampling obviously resulted in reduced species numbers as well as coverage, nevertheless, only small variations of H' and evenness could be found. Moreover, the undisturbed sites showed lower evenness values than the disturbed ones and caused a low value for H'.

Table 2 summarizes the most important diversity parameters for three plots on one tertiary dune in Karlshagen (site 4). On undisturbed tertiary dunes plant succession will lead to more mature plant communities than on primary and secondary dunes: more species are present and especially mosses and lichens play an important role within the ecosystem

Table 1
Examples of five different primary dune communities

Species	Site 4 (Karlshagen) 09.09.2003			Site 2 (Between Trassenheide and Karlshagen) 07.09.2003	
	1	2	3	4	5
Signs of trampling	Yes	No	Yes	No	Yes
Ammophila arenaria	0.5	0.50	0.50		
Festuca rubra	0.5	8.50			1
Salsola kali	1.5	3.50	1.50		0.2
Leymus arenarius	1.5	1.50	0.50	0.5	0.5
x Calammophila baltica	1.5	8.50	0.50		
Lactuca tatarica	0.5	0.50	1.50		
Petasites spurius				19.25	
Summed coverage	6	23.00	4.50	39	2.2
Species number	6	6	5	3	4
H'	1.661	1.367	1.465	0.753	1.250
H'_{dune}	0.268	0.652	0.205	0.661	0.111
E	0.927	0.763	0.910	0.685	0.902
$H'_{dune-max}$	0.276	0.750	0.212	0.796	0.114
E_{dune}	0.972	0.870	0.969	0.831	0.974

Numbers 1, 2, 3, 4 and 5 in the header represent plot numbers. All species and their coverage percentages (%) according to the scale from Barkman et al. (1964) are shown.

Table 2
Comparison of diversity indices on grey dunes with different levels of mechanical damages (level of impact)

Location	Site 4 Karlshagen	Site 4 Karlshagen	Site 4 Karlshagen
Plot number	6	7	8
Signs of trampling	Few	Many	Few
Total coverage	88.95	25.5	70.45
Number of species	24	12	23
H'_{dune}	1.54526526	0.94030468	2.07258017
H'	1.62013331	2.32097762	2.59164954
E_{dune}	0.52720795	0.95743649	0.84398109
E	0.50978787	0.9340301	0.82655217
$H'_{dune-max}$	2.93103557	0.98210659	2.45571874

For three neighbouring communities (site 12, holiday resort of Karlshagen) measured and calculated diversity parameters are shown. Areas with a high level of trampling alternate with other areas not showing any signs of mechanical disturbance.

(Isermann, 1997; Hesp, 1991). The data in Table 2 was taken from site 4 (Karlshagen), because it reflects the mosaic pattern of different levels of mechanical influence on that particular dune. Even though

(A)

(B)

Fig. 5. View of tertiary dunes. (a) Site 4 within the holiday resort of Karlshagen (July 2003) showing heavy signs of trampling. (b) Site 2 between Trassenheide and Karlshagen (August 2003) with very few visitors.

mechanical stress was not measured directly, the presence of illegal fire sites, garbage, and different footpaths supports this assumption. Since all plots are within the same part of the dune, they should have a similar potential for natural diversity and any differences are likely to be the result of anthropogenic change. Thus the plots shown are used as typical examples for the two extreme situations ''heavy'' and ''little'' mechanical disturbance.

The effects of evenness and species richness on H' illustrate how it fails to detect different levels of mechanical disturbance. Similar to the results shown in Table 1, H' mostly responds to changes in evenness. Changes in species richness are not reflected adequately, even though authors have favoured H' for its sensitivity in respect to rare species (e.g. Magurran, 1988). Plot number 7 (with 12 species and a very low coverage, because of trampling) has a much higher diversity according to H' compared to plot number 6. The weight H' puts on evenness becomes even more clear looking at plot number 8 which has roughly the same species richness as plot number 6, but a very high evenness value. Changes in coverage and species richness, which are both influenced by trampling, are not reflected by H' (Fig. 5).

3.2. Calculating and using H'—community models

To evaluate the weight H' puts on evenness, examples of communities with different total coverage, numbers of species and abundances were constructed. Fig. 6 summarizes the main parameters of these theoretical communities and shows their
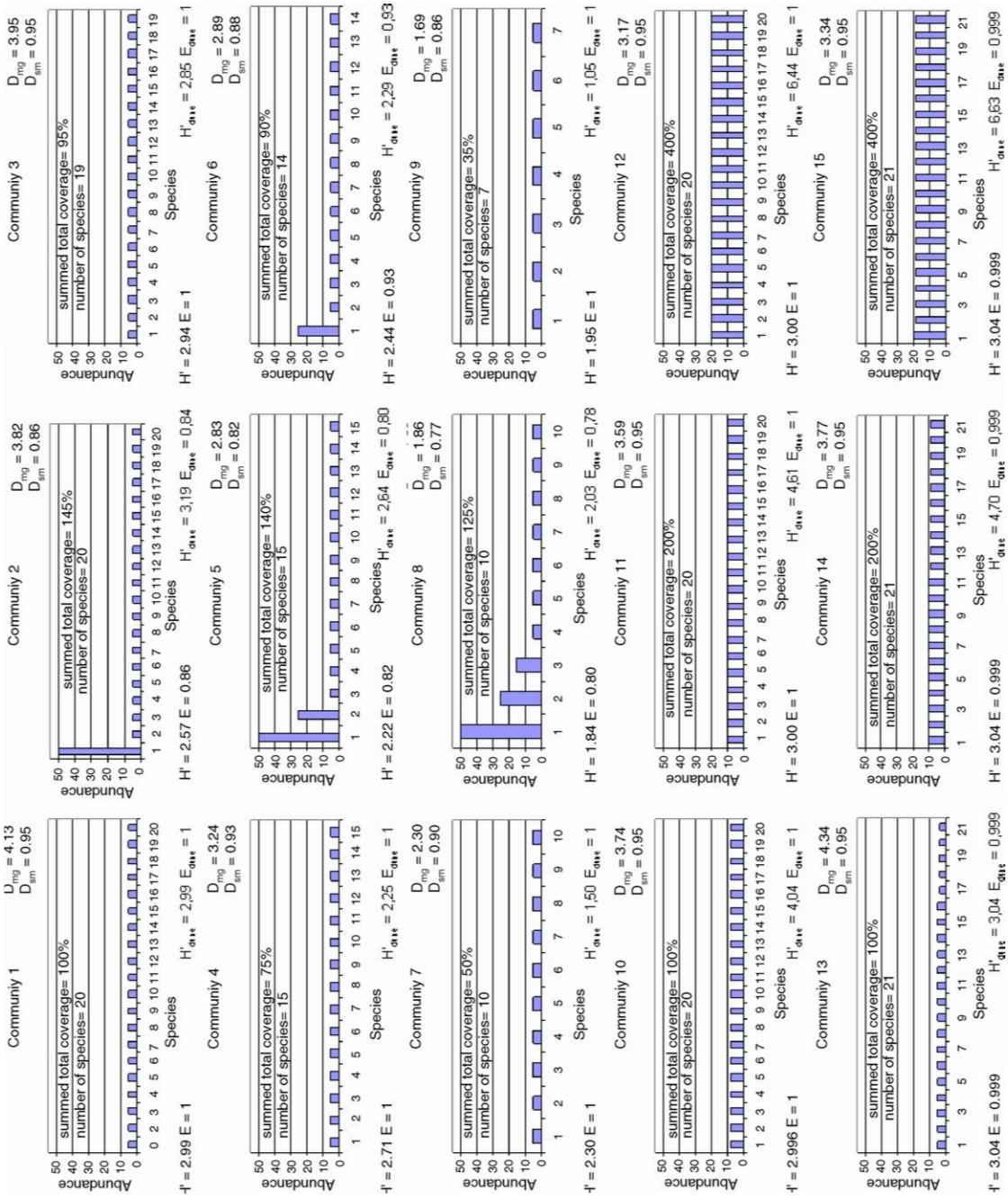
Fig. 6. Different community models for comparison of H' and H'_{dune} and how they are influenced by evenness, species richness and plant cover (D_{mg} = species richness index by Margalef; D_{sim} = diversity index by Simpson).

species abundance patterns. Communities C1, C4 and C7 show how H' decreases, if species richness decreases—in these examples evenness is kept constant at its maximum (1). Looking at the community groups C1, C2, C3 or C4, C5, C6 or C7, C8, C9 the way H' reacts to changes in evenness (one or more species become dominant and evenness decreases) is analyzed. C2, C5 as well as C8 all show decreasing H' values respectively to C1, C4 and C7 even though there is no absolute loss in species. The total coverage actually increased. In the communities C3, C6 and C9 dominant species were deleted, evenness again increased and so did H'. Species density (coverage) as well as species numbers decreased, but H' still "measures" a higher diversity.

As stated already above, H' very sensitively reacts on changes in evenness, whereas changes in total coverage are not reflected. Hobohm and Petersen (1999) as well as Haeupler (1982) already stated the strong weight H' puts on evenness. The most drastic example for this is given by comparing C8 with C9. From C8 to C9 three species became "extinct" without any other changes; however, H' was higher in C9 than in C8 where these species were the most abundant. Such species-poor communities are typical for many dunes (Table 1; Grunewald, 2004a,b).

This problem can be overcome in part by application of an index focusing on species richness alone, e.g. Margalef (D_{mg}), which is also shown in Fig. 6. However, because coverage is not included at all, effects of mechanical disturbance as shown in Fig. 6 (e.g. from C2 to C1) would not be reflected. Simpson's index ($D_{sim} = 1 - \sum P_i^2$) is often used as an alternative to H', but it also cannot overcome this problem (Fig. 6). By squaring the relative abundance of each species, dominant species also dominate the index (D_{sim} can be seen as a dominance index, Magurran, 1988); hence, Simpson's index also has a restricted sensitivity for species richness and the comparison of C7, C8 and C9 show similar results as for H'.

For the study of human change in species poor dunal systems a fine resolution of both parameters, relative abundance of each species and species number in any diversity index is required. In addition, a formula must be constructed which prevents the loss of information on total coverage (species density). The common way to calculate H' (Magurran, 1988) involves a normalization step by converting total abundances into relative (%).

The specific protocol given by Haeupler (1982) for plant communities also calls for this procedure and information on species density or species coverage is lost in the calculation of H'.

3.3. The adapted H'_{dune}—an attempt to overcome these problems by theory

Since the calculation of p_i relative to the summed total coverage is responsible for the way H' reacts to changes in coverage, the index was again calculated using the coverage percentage $P_{i\text{-dune}}$. This value is an abundance or coverage estimate for each species relative to the constant sample or plot size (and not to the summed total coverage of all species, Fig. 2). This new index (H'_{dune}) should now follow the rationale that when biomass and/or species richness decreases substantially as a result of trampling, the index must not increase as a result of an increase in evenness, but must decrease. In other words: A species with 5% cover in a plot will be rated the same in any community, regardless of other species presence or absence.

Fig. 7a shows the effects of increasing coverage values and increasing evenness values for 100 theoretical communities. Species richness (10 species) is kept constant. Very unevenly distributed communities slowly increase in evenness along the z-axis towards the back of the graph. From the left towards the right side of the graph the plant cover increases along the x-axis and so does in most cases the index. This is not true for very unevenly distributed communities (front row) which is due the fact that the limit of LN($P_{i\text{-dune}}$) is "0" and as soon as LN($P_{i\text{-dune}}$) reaches values above "−1" (above a coverage of approx. 40% for the dominant species) the index will slightly decrease again.[2] Using a different base/logarithm may partly solve this problem, but a decrease will still occur. On the other hand the steepness of the curve (the weight H'_{dune} puts on coverage and/or evenness) will be different. This problem may be overcome by substituting the term LN(P_i) with [(LN(P_i)) − 1] which has a limit of "−1" (Fig. 7b). Since testing field data did not reveal significant differences between both versions of the

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[2] The logarithmic term will lead to similar effects in the calculation of H', since the second normalization may lead to equivalent values for p_i as for $p_{i\text{-dune}}$; however, the changes in evenness will cover up such an effect.
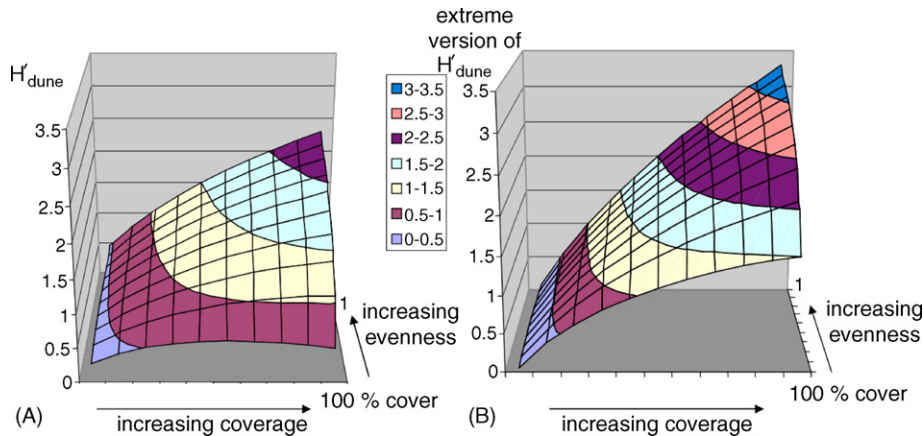
Fig. 7. How evenness and increasing plant cover affect: (A) the adapted index H'_{dune} and (B) the extreme version of H'_{dune}; H'_{dune} and an extreme version of H'_{dune} were analyzed using changing species abundance patterns. One hundred theoretical communities with a constant species richness of 10 species were used. Evenness is being increased along the *x*-axis and coverage increases along the *y*-axis. The *z*-axis shows the calculated diversity index and how it reacts to changes in coverage and evenness.

index (even in the species poor dune communities), the simpler version was used in this study.

Figs. 6 and 7 show that H'_{dune}, in contrast to H', reflects the effects of differences in coverage (species density). Evenness (E_{dune}) calculated using H'_{dune} remains independent from both species richness ($n = 429$ plots: $r^2 = 0.034$)[3] and coverage ($r^2 = 0.170$).[4]

Using H'_{dune}, C15 now is rated highest since it has the highest species richness and biomass/cover, the later can also be seen as an important element of diversity as well as ecosystem stability (especially on dunes). Looking at values for evenness, both calculations (using H' or H'_{dune}) give similar values and E_{dune} does fulfill the two most important properties of the conventional E:

- A maximum value of one can only be reached if all species have the same abundance.
- E_{dune} is independent of biomass/plant cover and species richness

Very slight changes in evenness are detected by E_{dune} as well as by E (C13–15). Looking at C1, C10 and C13, C11 and C14 and at C12 and C15 shows that evenness is

still an important part of the index, but H'_{dune} is more weighed towards species richness and coverage—evenness becomes important for discriminating between communities roughly sharing the same number of species and a similar total coverage. This is shown by comparing the community pairs above and then looking at the independent indices for evenness (E_{dune}) and species richness (Margalef). A single species community will have a maximum E_{dune} (1).

3.4. Application of the new formula on the field data

Using the new index H'_{dune} the data presented was again analyzed (Tables 1 and 2). It is now possible to clearly distinguish between the different sites and their different levels of anthropogenic impacts. H'_{dune} seems to clearly detect changes in species richness as well as density (coverage). In the following H'_{dune} was tested and used to compare different sites from Usedom and Wolin Island.

3.4.1. Results primary and secondary dunes

Figs. 8 and 9 show box and whisker plots for H'_{dune} and H' from primary and secondary dunes on Usedom Island. The boxes represent the second and third quartiles, the bar within the boxes indicates the median and whiskers indicate the smallest values within 1.5 interquartile ranges of the bottom. Small dots indicate

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[3] Results are taken from plots from several dune sites on Usedom and Wolin Islands, not only the sites presented in this paper.

[4] Testing correlation of E (using H') with species richness: $r^2 = 0.138$ testing E (using H') with coverage: $r^2 = 0.0128$.
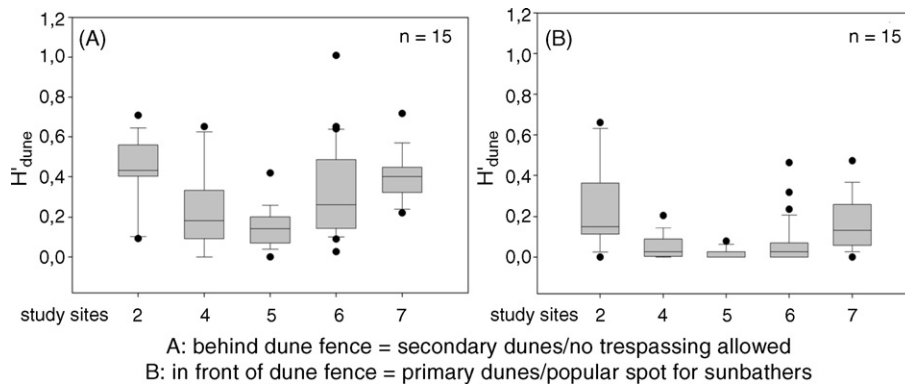
Fig. 8. Comparison of primary and secondary dunes with different levels of recreational activities using H'_{dune}. The protective dune fence was used as a reference line between the upper and lower plots. The boxes represent the second and third quartiles, the bar within the boxes indicates the median and whiskers show the standard deviation. Small dots indicate extreme values (2 = between Trassenheide and Karlshagen, undisturbed (no BM); 4 = Karlshagen, northern resort (BM); 5 = between Karlshagen and Parking (no BM); 6 = Parking, north of Karlshagen (BM); 7 = north of Parking (no BM)).
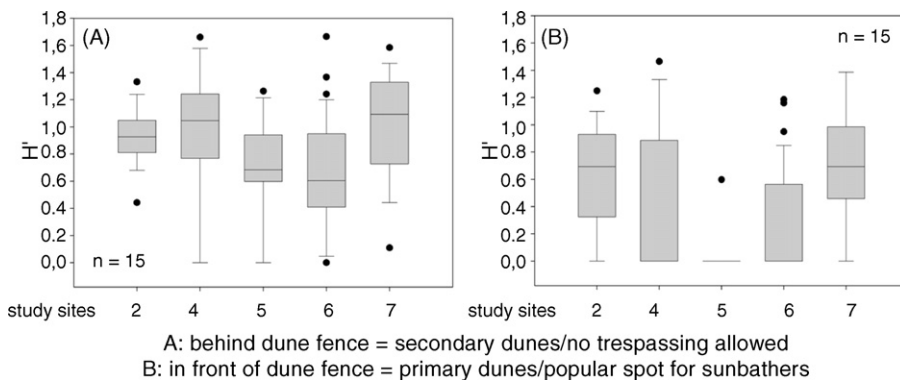

Fig. 9. Comparison of primary and secondary dunes with different levels of recreational activities using the diversity index H' (Shannon, 1949). The protective dune fence was used as a reference line between the upper (A) and lower plots (B). The boxes represent the second and third quartiles, the bar within the boxes indicates the median and whiskers show the standard deviation. Small dots indicate extreme values (2 = between Trassenheide and Karlshagen, undisturbed (no BM); 4 = Karlshagen, northern resort (BM); 5 = between Karlshagen and Parking (no BM); 6 = Parking, north of Karlshagen (BM); 7 = north of Parking (no BM)).

extreme values which fall outside the whiskers. The mean (m) and the number of plots documented at each site (n) are also given in the figures.

A statistical analysis (t-test, Kruskal–Wallis One-way Analysis of Variance on Ranks, all pairwise multiple comparison test) shows that there are significant differences ($p < 0.05$) between and within the sites (above and below the dune fence). Both H' as well as H'_{dune} detect significant differences between the upper and lower plots in most sites, only H'_{dune} does so at the site "Northern Beach".

The comparison between the sites is the second method of discriminating the sites and assessing human impact: Table 3A and B shows the results of a one-way ANOVA on ranks for both H' and H'_{dune}.

3.4.2. Results tertiary dunes

Figs. 10 and 11 show the use of H'_{dune} and H' comparing a total of 119 plots from 5 different sites on Usedom and Wolin Islands (Germany and Poland). The box and whisker plots reveal the main characteristics of the different sites including mean (m) and

Table 3
Results of a one-way ANOVA on ranks for both H' (A) and H'_{dune} (B) for primary and secondary dunes

A

H'	2 Trassenheide undisturbed	4 Karlshagen resort center	5 north of Karlshagent	6 Beachside Parking	7 Northern beach	H' above dune fence
2 Trassenheide undisturbed	above / below	No	No	No	No	2 Trassenheide undisturbed
4 Karlshagen resort center	No	above / below	No	No	No	4 Karlshagen resort center
5 north of Karlshagent	Yes	No	above / below	No	No	5 north of Karlshagent
6 Beachside Parking	Yes	No	No	above / below	No	6 Beachside Parking
7 Northern beach	No	No	Yes	Yes	above / below	7 Northern beach
H' below dune fence	2 Trassenheide undisturbed	4 Karlshagen resort center	5 north of Karlshagent	6 Beachside Parking	7 Northern beach	above / below

B

H'_{dune}	2 Trassenheide undisturbed	4 Karlshagen resort center	5 north of Karlshagent	6 Beachside Parking	7 Northern beach	H'_{dune} above dune fence
2 Trassenheide undisturbed	above / below	Yes	Yes	No	No	2 Trassenheide undisturbed
4 Karlshagen resort center	No	above / below	No	No	No	4 Karlshagen resort center
5 north of Karlshagent	Yes	No	above / below	No	Yes	5 north of Karlshagent
6 Beachside Parking	Yes	No	No	above / below	No	6 Beachside Parking
7 Northern beach	Yes	No	Yes	Yes	above / below	7 Northern beach
H'_{dune} below dune fence	2 Trassenheide undisturbed	4 Karlshagen resort center	5 north of Karlshagent	6 Beachside Parking	7 Northern beach	above / below

Significant differences are indicated with "yes". Insignificant differences are indicated with "no" ($p < 0.05$).

number of analysed plots per site (n). The boxes represent the second and third quartiles, the bar within the boxes indicates the median and whiskers indicate the smallest values within 1.5 interquartile ranges of the bottom. Small dots indicate extreme values which fall outside the whiskers. The mean (m) and the number of plots documented at each site (n) are also given in the figures.

Mean values show strong differences between the sites, and a statistical analysis (t-test, Kruskal–Wallis
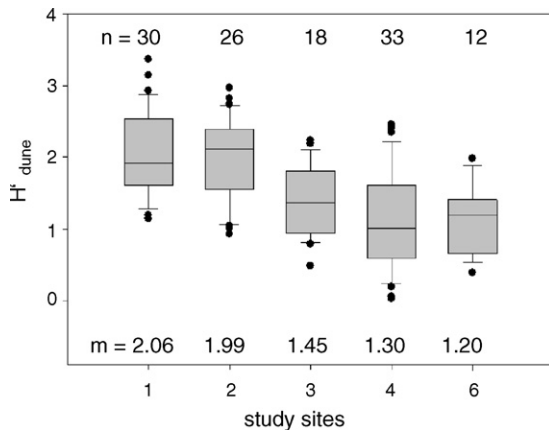
Fig. 10. Comparison of tertiary dunes with different levels of recreational activities using H'_{dune} (n = number of plots per site, m = mean value per site) (1 = Wolin, undisturbed; 2 = between Trassenheide and Karlshagen, undisturbed (no BM); 3 = Karlshagen, Camping (BM); 4 = Karlshagen, northern resort (BM); 6 = Parking, north of Karlshagen (BM)).
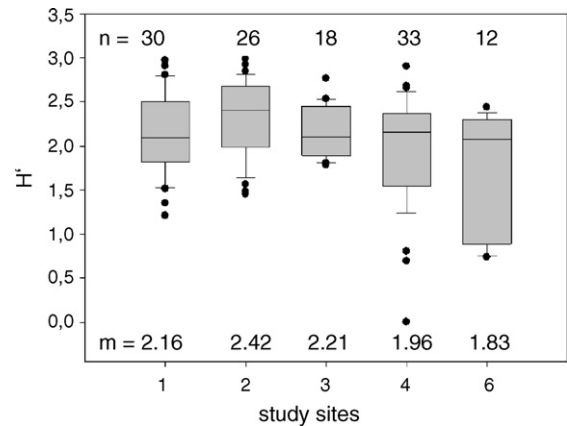

Fig. 11. Comparison of tertiary dunes with different levels of recreational activities using H' (n = number of plots per site, m = mean value per site) (1 = Wolin, undisturbed; 2 = between Trassenheide and Karlshagen, undisturbed (no BM); 3 = Karlshagen, Camping (BM); 4 = Karlshagen, northern resort (BM); 6 = Parking, north of Karlshagen (BM)).

One-way Analysis of Variance on Ranks, all pairwise multiple comparison test) reveal significant differences shown in Table 4.

The second important aspect for dune conservation (tertiary dunes) is species composition: How many untypical species occur on the dunes and how dominant are these species? This degree of natural diversity (N) is shown in Fig. 12 (formula given in

Fig. 2). The maximum value for N is one, since the natural diversity cannot be higher than the complete diversity using H'_{dune} (using H' there may be an increase in natural diversity, if untypical species are left out of the calculation like it was done in Fig. 6: C2 and C3, C5 and C6, C8 and C9). Significant differences between sites are shown in Table 4.

Table 4
Results of a one-way ANOVA on ranks for tertiary dunes

H' and H'$_{dune}$ / N	1 Wolin Undisturbed	2 Trassenheide – undisturbed	3 Karlshagen Camping	4 Karlshagen, resort	6 Parking	H'$_{dune}$ / H'
Wolin Undisturbed		no	yes / no	yes / no	yes / no	1
Trassenheide– undisturbed	no		no	yes / no	no	2
Karlshagen Camping	yes	yes		no	no	3
Karlshagen, resort	yes	yes	no		no	4
Parking	yes	yes	no	no		6
N (degree of natural diversity)	Wolin Undisturbed 1	Trassenheide – undisturbed 2	Karlshagen Camping 3	Karlshagen, resort 4	Parking 6	H' and H'$_{dune}$ / N

In the upper right half results from both H' (A) and H'_{dune} (B) are shown. In the lower left half results for the degree of natural diversity are given. Significant differences are indicated with "yes". Insignificant differences are indicated with "no" ($p < 0.05$).
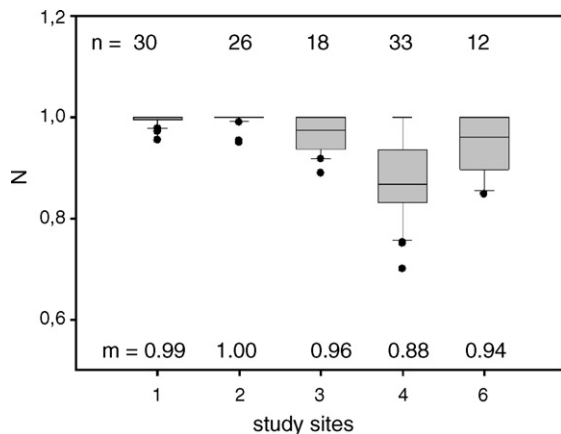
Fig. 12. Comparison of tertiary dunes with different levels of recreational activities using the degree of typical dune species (natural diversity) present in relation to the overall diversity (Fig. 9). This ratio was used as a measure of the degree of natural diversity (N) (n = number of plots per site, m = mean value per site) (1 = Wolin, undisturbed; 2 = between Trassenheide and Karlshagen, undisturbed (no BM); 3 = Karlshagen, Camping (BM); 4 = Karlshagen, northern resort (BM); 6 = Parking, north of Karlshagen (BM)).

3.4.3. Discussion
Main properties of H' and H'_{dune}

Testing H' and H'_{dune} and the parameters important for biodiversity (species richness, evenness, and species density) were conducted using 429 different plots from primary, secondary and tertiary dunes on Usedom and Wolin Island (including data from sites not presented in this paper). Correlation coefficients between these three parameters and H'_{dune} as well as H' were calculated.

As expected using all 429 plots evenness and species richness both correlate with H' (evenness: $r^2 = 0.21$, Pearson correlation coefficient = 0.714 and species richness: $r^2 = 0.77$, Pearson correlation coefficient = 0.920). However; the correlation shows important differences when data from tertiary dunes and secondary and primary dunes are analysed separately: For species poor secondary and primary dunes ($n = 180$, $r^2 = 0.75$, Pearson correlation coefficient = 0.882) the correlation of evenness with H' is much stronger than for species rich tertiary dunes ($n = 249$, $r^2 = 0.136$, Pearson correlation coefficient = 0.766). The separate analysis of correlation between species richness and H' (secondary and primary dunes: $n = 180$, $r^2 = 0.76$, Pearson correlation coefficient = 0.877 and for tertiary dunes: $n = 249$,

$r^2 = 0.16$, Pearson correlation coefficient = 0.788) shows that species richness does not correlate as strongly with H' on tertiary dunes (high number of species, high evenness, high coverage) than it does on primary and secondary dunes (low number of species, low coverage). Evenness seems to be the dominating factor in communities with low coverage values which was also shown in Tables 1 and 2.

Total coverage exhibits a strong correlation with species richness ($n = 429$, $r^2 = 0.71$, Pearson correlation coefficient = 0.881) and cross-correlates with H' as well ($n = 429$, $r^2 = 0.55$, Pearson correlation coefficient = 0.747). This may be explained by the fact that higher coverage values are mostly found on tertiary dunes which also have higher species richness than primary or secondary dunes with lower coverage. The correlation between cover and H' is much weaker, when only data from primary and secondary dunes is used ($n = 180$; $r^2 = 0.07$, Pearson correlation coefficient = 0.327) or only data from tertiary dunes ($n = 249$, $r^2 = 0.09$, Pearson correlation coefficient = 0.330). This shows that information on species density is being lost in the calculation of H'.

The correlation between H' and H'_{dune} was also tested using data from primary, secondary and tertiary dunes and revealed a strong correlation of the two tested parameters ($n = 429$, $r^2 = 0.77$, Pearson correlation coefficient = 0.876). However, when only tertiary dunes or only secondary and primary dunes are being compared, the correlation differs a lot (tertiary dunes: $n = 249$, $r^2 = 0.50$, Pearson correlation coefficient = 0.705 and primary and secondary dunes: $n = 180$; $r^2 = 0.25$, Pearson correlation coefficient = 0.498). In the species poor communities with low coverage the differences between the two indices become evident. Once plant succession has led to more complex plant communities with higher coverage values both indices start to correlate more. It is obvious, that the closer the summed total coverage is to 100%, the more similar H' and H'_{dune} will be. This shows that the present use of H' may be restricted to saturated communities (high coverage) where inter species competition is the dominant factor for species presence or absence. Whenever total cover is not close to 100% H' will be dominated by the factor evenness.

Peet (1974) calls H' a heterogeneity index and Haeupler (1982) and Hobohm (2000) criticise the strong weight of evenness in calculating H' and do not

propose its broad use as a general diversity indicator. Instead they propose to use evenness, because it is independent of species richness and calculate typical evenness values for different communities. The strong influence of evenness on H' was shown by their strong correlation. Nevertheless, the problem of species density has been largely neglected and only little information was found in literature (e.g. Pielou, 1966). Instead, in many studies H' and absolute cover are calculated and analysed separately (e.g. Rodgers, 2002; Andersen, 1995).

Because of the strong weight of evenness, H' is only a measure for relative diversity in respect to the maximum possible diversity for one specific community at one specific time (see also Shannon and Weaver, 1949; p. 8: "To be sure, this word information in communication theory relates not so much to what you say, as to what you could say. That is, information is a measure of one's freedom of choice when one selects a message."). According to Shannon ", the amount of information is defined, in the simplest cases, to be measured by the logarithm of the number of available choices . . ." (Shannon and Weaver, 1949; p. 9). Hence, there is the need to define the number of available choices (=sample size).

So far, using H' in biological diversity studies this was the total number of individuals sampled or the summed total coverage (amount of biomass) of all plant species, Haeupler, 1982; Magurran, 1988; Townsend et al., 2002). Whenever total coverage is used as the definition of sample size, then this number of available choices must be kept constant. Communities saturated with species and individuals (inter-species competition as the driving force of species presence or absence) may roughly meet this requirement since the total cover will be around 100%. If disturbance like trampling leads to a reduction of total cover, the sample size has substantially changed making an analysis of disturbance using H' very difficult. As shown in Tables 1 and 2, the total plant cover or species density is not constant, but varies a lot as a result of human impact. In Table 2 plots 6 and 8 roughly share the same species number, but differ in evenness and cover, because of damage from trampling in plot 8. The information on species density is being lost once the abundance of species relative to summed total coverage is calculated and evenness will dominate the index. Therefore, H' is not

a straightforward approach for comparing diversity between different sites and not even the same site at different times, because the sample size is not kept constant.

For H'_{dune} a different way was chosen to make sure the number of available choices (=sample size) will be kept constant. Magurran (1988) describes common definitions of sample size.

- Number of individuals sampled (or coverage/biomass).
- Area of sampling.
- Time for sampling.

Studying plant communities the habitat (minimum area) can be completely sampled so that time as a measure of sample size (sampling effort) can theoretically be neglected.

The remaining two parameters (coverage and area) can each be seen as one dimension of sample size using H'. It is an important difference, if one samples 200 individuals in an area of 100 m^2 or 200 individuals are found within 10 m^2. It is also a huge difference, if 100 individuals or 200 individuals are found within 10 m^2. In other words: Information on species density and on species presence or absence is important.

The different way H'_{dune} is calculated does not omit the parameter species density, but defines it as a parameter of species diversity itself. For each species, its density is not related to the other species present, but to the habitat it grows in. Thus, the sample area can be defined as the sole basis of comparison (="number of available choices", Shannon and Weaver, 1949). The inclusion of coverage (species density) into the calculation of H'_{dune} creates a counterweight to the very dominant factor evenness. In H'_{dune}, evenness is used to differentiate between communities sharing similar numbers of species and comparable coverage values (Table 2). Evenness (E_{dune}) can be easily calculated in a similar way as E (evenness using H', Fig. 3). It is independent from both total coverage and species richness and is a much better index for analyzing community structure than H' as it was already shown by Haeupler (1981). Table 2 as well as Fig. 6 show that E and E_{dune} differ very little. The main differences are single species stands: H' does not differentiate between no species or single species stands and cannot be calculated in such situations.

H'_{dune} can be calculated for single species stands and E_{dune} will have a value of one. Once these single species stands are left out, E (evenness using H') and E_{dune} (using H'_{dune}) strongly correlate ($n = 397$, $r^2 = 0.77$, Pearson correlation coefficient $= 0.880$). This enables users of H'_{dune} to also use E_{dune} for their community analysis.

Using H'_{dune} for the detection of human changes on coastal dunes

Applying H'_{dune} on the field data, the greater sensibility of H'_{dune} for changes is revealed for primary and secondary dunes at the most northern site (7), where only few heavily trampled pockets of bare sand exist, which are only detected by H'_{dune}. One important difference between H' and H'_{dune} is the value for mono-species stands: In such cases H'_{dune}, in contrast to H', is able to differentiate with respect to their different coverage.

The statistical analysis between different secondary dunes shows that H' does not detect any significant differences between sites behind the dune fence (Fig. 9 and Table 3). Using H'_{dune} the low coverage values are not neglected and changes between the remote sites (less people = less disturbance) 2 and 7 on one side and the heavily used sites in and around Karlshagen are significant (Fig. 8 and Table 3). In front of the dune fence the situation becomes clearer and the effects of tourists and beach management are obvious: H' detects the great differences between the undisturbed sites and the heavily used sites, but H'_{dune} detects a further difference between site 2 and the almost bare sand at site 4 (Karlshagen, Resort Center).

The mean values of H'_{dune} can also be used to further discriminate the sites. Above and below the dune fence in site 4 (Karlshagen) H'_{dune} detects damage from trampling which results in a low mean. On the other hand the mean values in site 2 (between Trassenheide and Karlshagen) are slightly higher than at "Northern Beach".

For tertiary dunes H'_{dune} detects significant changes between site 1 on Wolin (undisturbed) and site 2 (between Trassenheide and Karlshagen) on one side and the heavily disturbed sites in and north of the holiday resort of Karlshagen. H' was only able to differentiate for 50% of those sites.

Aside coverage effects, mostly caused by mechanical damage, qualitative changes in plant community composition were observed especially in tertiary dunes. Similar findings were made by Rodgers (2002) and Piotrowska (1988). Specialized species are driven out because of a rise in nutrients and an invasion of ubiquist species. Therefore a classification of the species with respect to natural diversity and naturalness (N) was needed. Such a classification of species is a common procedure in ecological and conservational studies (e.g. Grime, 2002; García-Mora et al., 2000, 2001; Martinez and Psuty, 2004; Rodgers and Parker, 2003; Rodgers, 2002). The rise in more ubiquist or ruderal species may be explained by a rise in nutrients on tertiary dunes and by gardening activities in the vicinity of holiday resorts like Karlshagen (site 4). Neighbouring effects from public and private gardens adjacent to dunes may be another explanation. Habitats can only be settled by species which are able to reach this habitat, as was shown by Pärtel et al. (1996). The species pool of the area around the studied habitat (regional species pool) influences species diversity in the habitat itself. According to the species pool hypothesis, holiday resorts would have a larger species pool and influence the diversity on the adjacent dunes; nevertheless both explanations are linked to tourism or anthropogenic change in general and both are likely to jointly influence species diversity on the dunes. The low number of ruderal species at site 3 (campground south of Karlshagen) and site 6 (Parking) may indicate the importance of the species pool, but the level of control at site 3 (campground with life guards on the beach and campground staff) is quite high, so that not many people trespass the dunes. Public toilets are available at site 3 as well, so that the level of disturbance on the dunes is generally quite low. At site 6 the situation is similar: the dunes are easily overlooked from the access pathways to the beach and only very few bushes and trees provide some shelter for tourists defecating on the dunes. Most will walk further into the coastal pine forest, where a number of ruderal species indicate higher nutrient levels and eutrophication (e.g. *Sambucus nigra*, *Urtica dioica*). These areas in the coastal forest however were not studied.

For tertiary dunes, mosses and lichens have been shown to be major components of plant diversity, Piotrowska (1979) states that 50% of the total number of plant species are either mosses or lichens. In the present study they accounted on average (!) for 44% of the

diversity on grey dunes (including disturbed plots). Haeupler (1981) does not include mosses and lichens into his analysis and uses the following two arguments.

1. The level and quality of species identifications varies between scientists and more problematic groups should therefore be excluded.
2. Even though cryptogams make up an important amount of diversity they often create a separate vegetation layer and should be analysed separately.

Since in this study species identification was conducted by one single scientist and critical species were crosschecked by experts the first argument can be neglected for this study. An alternative to circumvent the problem would be pooling of all pedogenic lichens and separately all mosses into two functional groups, giving not the same, but clearly better results than neglecting these organisms. According to Piotrowska (1979) cryptogamic plant communities show little resistances against mechanical stress and moreover have only little power of fast regeneration; hence, it is very important to include them in the study. The second argument can also be countered by proposing to calculate indices according to ''functional groups'' (grasses, herbs, dwarf shrubs, other shrubs, C4 species, etc.) as done successfully for dunes, other terrestrial communities or aquatic habitats by, e.g. García Novo et al., 2004; Hellemaa, 1998; García-Mora et al., 2000, 2001.

4. Conclusions

The present study shows that the common assumption that H' (species number and abundance relative to the total abundance) is an appropriate estimate for diversity cannot be followed for unsaturated and/or disturbed systems with low plant cover and/or changing cover. In these calculations the sample size is not kept constant. H' is a measure of diversity relative to the maximum diversity possible for the number of species present in each site and hence in strongly dominated by evenness. Therefore, H' is not sensitive for changes, because of human influence. Incorporating coverage as a term influencing diversity, as done in the present case, overcomes this problem. Applying this new concept on the

detection of anthropogenic changes on dunes showed the applicability of this index H'_{dune} and therefore verifies the assumption that coverage (species density) should be included into diversity studies. The new index has been shown to allow for calculation of evenness (E_{dune}) in a similar way as H'.

A second potential degradation factor for dunal ecosystems is a human induced rise in nutrients and or neighboring effects from nearby gardens and parks, leading to increased plant coverage and invasion of ubiquist or ruderal species. Such effects have been described in literature (Cornell, 1999; Pärtel et al., 1996), but cannot be detected by means of H' or H'_{dune} alone and therefore require the use of a classification system, discriminating between ''typical'' and ''non typical'' dune species. The resulting calculation of the degree of natural diversity in the different dune communities (naturalness = N) revealed qualitative changes in dunal species composition.

The use of H'_{dune} may not be restricted to coastal habitats and seems likely to be applicable in other habitats as well. So far, this has not been tested.

Acknowledgements

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