Statistical Measures of Fidelity Applied to Diagnostic Species in Plant Sociology

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Abstract

The idea of a diagnostic species is an important concept in plant sociology. However, since over a century ago, when the term "association" was introduced, the identification of diagnostic species has been among the most controversial topics in phytosociological practice. With the aim of promoting methodological standardization in plant sociology, this paper addresses: 1) the need to distinguish between the concepts and methods involved in the definition of syntaxa (analysing relevés, characterization, diagnosis, naming and typification), and 2) the need to support and improve existing syntaxonomical classification schemes using statistical measures of fidelity to identify diagnostic species. The phytosociological literature describes numerous different approaches to the designation of diagnostic species. Here, we examine two such approaches to determine diagnostic species using as an example the class *Atriplici julaceae-Frankenietea palmeri* within the context of a data set of 5092 relevés taken of coastal plant communities distributed along the Pacific rim of North America. Diagnostic species were determined using both the phi-coefficient of association to detect differential species and the Ochiai index to designate character species. Our findings support the results obtained by combining classic phytosociological methods (expert knowledge, rearrangement of relevé tables, presence tables, etc.) with clustering methods.

Keywords: association, diagnostic species, fidelity measures, ochiai index, phi-coefficient, vegetation classification

1. Introduction

Over one hundred years have passed since the Third International Botanical Congress held in Brussels in 1910 coined the first formal definition of the plant association, which marked the birth of plant sociology (Blasi, Biondi, & Izco, 2011). At the congress, amidst intense dispute between plant sociologists and physiognomists, Flahault and Schröter obtained unanimous approval for a definition of association as an abstract vegetation unit that features: 1) a definite floristic composition, 2) a uniform physiognomy, and (3) its occurrence in uniform habitat conditions (Flahault & Schröter, 1910). Given its complete nature, this definition continues to be valid. Indeed, in his revision of the phytosociological association concept, Willner (2006) suggested going back to Flahaut and Schröter's definition, and a similar definition of association was provided by the US National Vegetation Classification (Jennings, Faber-Langendoen, Loucks, Peet, & Roberts, 2009). Despite being such a comprehensive definition, there is still no consensus as to the practical application of the concept (Willner, 2006; Biondi, 2011). This is in large measure because the original concept required at least one clarification: What exactly is a "definite floristic composition"?

Three years after that congress, it was Braun-Blanquet who for the first time selected one characteristic feature of an species he termed "fidelity", as being the most valuable for association diagnosis (Braun-Blanquet & Furrer, 1913). By this, Braun-Blanquet refers to the complete or partial restriction of certain species of narrow ecological amplitude to one particular association. In later publications, however, Braun-Blanquet substantially modified his initial concept. First he introduced the "characteristic species combination" as the main feature for

the diagnosis of an association (Braun-Blanquet, 1925); and later he adopted Koch's (1926) idea of differential species to distinguish between two syntaxonomically related units and restricted the geographical validity of character species to relatively small and ecologically homogeneous regions (Braun-Blanquet & Moor, 1938).

Despite numerous discussions in congresses and meetings in the middle of the last century, a summary of which may be found in Westhoff and van der Maarel (1973: 625), ample consensus was reached for considering that the floristic composition that defines an association, and, by extension, the rest of syntaxonomic hierarchies, is comprised of a diagnostic species that includes character and differential species, along with constant companions. Thus, Syntaxonomy can be regarded as a hierarchy system whose units are defined by groups of diagnostic species and not only by its character species in the strict sense.

Plant communities can be viewed as a hypothesis that predicts the conditions of a habitat (or viceversa) within a given area (Pignatti, 1980). Floristic difference contains no useful information as long as it cannot be interpreted as a reflection of a different habitat or a different vegetation history. This is because one of the basic objectives of Syntaxonomy is to establish a hierarchical system reflecting the patterns of similarity and dissimilarity between vegetation types (Braun-Blanquet, 1964; Westhoff & van der Maarel, 1978) in an effort to reduce the diversity of vegetation to a level that is easily comprehensible by the human mind (Mirkin, 1989; Moravec, 1989), thus facilitating communication among plant scientists (Willner, 2006). The goal is analogous to that described by Stuessy (1997) for plant taxonomy: to provide "a biological classification of high predictive value".

The phytosociological literature contains numerous different approaches to the designation of diagnostic species. Frequently, these results in discrepancies between the lists of diagnostic species published for the same community (Chytrý et al., 2002b; Khan et al., 2013a). The fact that species differ in their diagnostic value is reflected in the concept of fidelity, i.e., the extent to which a species is concentrated in a given vegetation unit. The fidelity of a species determines whether it can be considered a differential or character species or just a companion or accidental species (Braun-Blanquet, 1918). The faithful species concept *sensu* Braun-Blanquet positions itself either in the context of a given phytogeographic unit whose extension may vary within conventional phytogeographic classification systems, or alternatively in the ecological context, which is similarly variable, given that a faithful species can be so, due to very broad factors (macroclimate or limestone soils would be two general examples) or highly specific factors (microclimate or microedaphic, for instance).

Despite its usefulness, the concept of fidelity has inherent an essential concept problem, the old Aristotelian dilemma of the circular argument: a vegetation unit is defined by diagnostic species (excluding constant companions) and at the same time diagnostic species are those that show a preference for this vegetation unit. Although this circularity is not resolvable using logical arguments (Poore, 1955), this does not prevent the quantification of fidelity from being optimised if valid algorithms are found to identify species with statistically significant fidelity values (Bruelheide, 2000; Khan et al., 2011) that support other numerical classification methods based on a full comparison of the floristic assemblage (De Cáceres & Wiser, 2011; Khan et al., 2013b).

2. Measures of Fidelity

In this section, the following terminology is used. Generally speaking, the reader may consider field observations as sampling units such as phytosociological relevés, or any other type of sampling unit that can be used in presence/absence data sets. Here, we distinguish between the syntaxa whose fidelity we wish to assess, or target syntaxa (TSY), and the remaining relevés of the data set, which will serve as samples to compare with. These samples are here designated as reference groups (REF).

The first quantitative method used to assess fidelity was described in detail by Szafer and Pawłowski (1927), who prepared a numerical table in which five fidelity classes were defined. With slight modifications, this table appears in almost every review and textbook of Phytosociology (Becking, 1957; Westhoff & van der Maarel, 1973; Braun-Blanquet, 1979; Dierschke, 1994). Although Szafer and Pawłowski's guide to fidelity was valid at the time, its shortcomings were well known and its practical application to select diagnostic species involved long optimization processes that included several subjective choices within different contexts (Koči, Chytrý, & Tichý, 2003). These shortcomings have been discussed in reports in which alternative measures of fidelity are proposed based on cover (Barkman, 1989), constancy or frequency (Bergmeier et al., 1990; Dengler, 2003) data. In general, although tables with numerous relevés were considered, these contained either ecologically-related syntaxa or ecologically and floristically different syntaxa within a reduced geographical area. In either case, such highly intuitive measures of fidelity were of low statistical value and poorly reliable (Chytrý & Otýpková, 2003).

A characteristic species can be interpreted as a special kind of differential species: a differential species may occur in one or more vegetation unit, whereas a characteristic species should occur in only a single vegetation unit (Barkman, 1989). In reality, both character species and differential species are types of diagnostic species

but viewed in different contexts (Chytrý, Tichý, Holt, & Botta-Dukát, 2002a; De Cáceres, Font, & Oliva, 2008). The context of differential species in the sense of Koch (1926) can be achieved in two main ways: (a) by comparing a given TSY using as REF immediately higher syntaxa: associations within their respective alliances, alliances within their respective orders and orders within their respective classes; or (b) using as REF the syntaxon that most resembles the TSY floristically, as proposed by Becking (1957: 447) and Barkman (1989: 109). Both approaches can be used to search out differential species among different syntaxa, but it should be noted that all species not included in such syntaxa will be excluded from the comparison, as will the rest of the vegetation units occurring in the area under study. As a result, the measure of fidelity of any species will be limited by its context: i.e., that of the vegetation units compared. If the species shows broad ecological amplitude, it could appear in other vegetation units not used as references and consequently its fidelity values will be of little statistical significance.

To circumvent this problem, if the number of relevés in the data set is maximized, this will both broaden the ecological and geographical context and we will only have to syntaxonomically delineate the TSY; the rest of the data set will serve as a reference unit without the need for its syntaxonomic organization. If, what is more, the method used to calculate fidelity is based on presence/absence data rather than a quantitative measure, we could even use as reference samplings comprising quantitative data obtained by methods that considerably differ from strictly phytosociological relevés, provided that deviations that could provoke differences in the sampling plot size are considered (Dengler, Löbel, & Dolnik, 2009).

Fidelity is a relative measure: it compares the presence of a given species within a given TSY with that of a REF. Working on cenological fidelity, Juhász-Nagy (1964) distinguished three forms of fidelity, which were summarized by De Cáceres et al. (2008) as: (1) the asymmetric fidelity of the TSY to the species, when all relevés belonging to the TSY contain the species; (2) the asymmetric fidelity of the species to the TSY, when the species occurs only in relevés belonging to the TSY; and (3) mutual fidelity, when both elements are symmetrically faithful to each other.

Optimal measures of fidelity are those that tend towards maximal symmetry, that is, to mutual fidelity (Dufrêne & Legendre, 1997). However, although special attention should be paid to mutual fidelity, the role of the ecological and geographical context also needs to be assessed, since the fidelity of diagnostic species statistically depends on the number of samples in the reference data set in that the more relevés used as references, the greater will be the statistical significance of the measure of fidelity. Hence, the first question to consider is how to determine the context in which to evaluate measures de fidelity.

The methods used traditionally by phytosociologists to select diagnostic species either limit the ecological setting and broaden the geographical setting (e.g., basophilic beech woods in Europe), or restrict the geographical context and expand the ecological setting (as usually done in phytosociological guides for a given region in which ecologically diverse communities are compared). In both cases, the diagnostic species will be delimited by one or the other context such that their validity as indicators will be poor, as will their statistical validity (Chytrý et al., 2002a, 2002b). Obviously, if we increase the number of samples used to compare with, the statistical significance of the diagnostic species detected will also increase.

Whatever the geographic setting, several criteria can be used to select the relevés to include in a reference data set (REF) with which we will compare the given target syntaxon (TSY). De Cáceres et al. (2008) propose the use of a dual strategy with two different objectives: 1) to detect differential species depending on the context, which was the criterion used by Becking (1957) and Barkman (1989); and 2) to assess the diagnostic value of the species regardless of the context such that this is as significant as possible, aimed at identifying the truly faithful diagnostic species, i.e., the character species.

To contextually search out differential species is interesting from a standpoint of syntaxonomic classification. However, the results are highly dependent on the context and, though fidelity measures are comparable against each other, they are not statistically representative and thus their predictive value as indicators is not too reliable. In contrast, fidelity analyses based on data sets for a high number of relevés fulfil the second objective and offer a significant diagnostic value within a given geographical setting, though they do not detect differential species. This problem is resolved by the combined use of the phi-coefficient and Ochiai index (*OI*) since the former detects the differential species, while the latter does so to find the diagnostic species within a given geographical context. Obviously, the greater the geographical context and the more ecologically diverse the syntaxa comprising the REF, the more representative will be the diagnostic species. If in addition these symmetric measures of fidelity are complemented with measures of asymmetric fidelity, an extremely reliable analysis is obtained of the character species of any syntaxon (Table 1).

Table 1. Summary of main features of the diagnostic species and the methods usable for their identification (Modified from De Cáceres et al., 2008)

Type	Statistical measure	Description
1.- Diagnostic species	Ochiai Index, OI, $\in [0.1]$	Any species whose presence or absence in a given vegetation unit can be used to indicate it belongs or not to a syntaxon.
1a.- Constant species	Constancy $c = n_p/N_p$, $\in [0.1]$	A species showing a significantly high frequency in a given TSY. Its diagnostic value derives from the fact that its absence is evidence for not assigning the type to the sampled community. In a non-strictly phytosociological context, it can also be called the "sensitivity" of the indicator.
1b.- Asymmetrically faithful species	Presence $p = n_p/n$, $\in [0.1]$	A species whose occurrence is significantly restricted within the faithful species communities of the target unit. Its diagnostic value derives from the fact that its presence in a sampled community provides a strong basis for assigning the unit to the community. This diagnostic value can also be referred to as a positive predictive value).
2. Differential species	ϕ-Coefficient, $\in [-1.1]$	A species whose presence in a given vegetation unit can be used to differentiate between that unit and similar types.

In this table and throughout the rest of this article, we use the same notations as Bruelheide (2000): N = total number of relevés of the whole data set (TSY + REF); N_p = number of relevés belonging to the TSY; n = number of species occurrences in the whole data set; n_p = number of species occurrences in the TSY.

2.1 The Phi-Coefficient of Association

Chytrý et al. (2002a) compared the different binary coefficients commonly used to determine mutual fidelity in plant communities and found that the index that provided the best results was the phi-coefficient of association (ϕ) defined by Sokal and Rohlf (1995):

$$\Phi = \frac{N \cdot n_p - n \cdot N_p}{\sqrt{n \cdot N_p \cdot (N - n) \cdot (N - N_p)}}$$

The phi-coefficient takes values ranging from -1 (maximum negative fidelity) and +1 (maximum positive fidelity). Positive values indicate that the species and the vegetation unit co-occur more frequently than would be expected by chance. Larger values indicate a greater degree of mutual fidelity. A value of 1 indicates that the species and the vegetation unit are completely faithful to each other, because ($np = n = Np$), i.e., the species occurs at all sites of the vegetation unit. For the identification of diagnostic species, positive Φ-values are of particular importance, although negative Φ-values can be also used for negative differentiation of community types, especially if there are not too many site groups in the given typology (Tichý & Chytrý, 2006; Khan et al., 2011).

The phi-coefficient depends on the size of the TSY (N_p), which may vary from 1 to (N - 1), and could lead to unreliable conclusions when the data sets contain site groups of unequal size, commonly found in the

phytosociological literature. Tichý and Chytrý (2006) resolved the problem by equalizing the size of the site group to the size of N_p for all the TSY within the data set (N), such that the fidelity measures obtained by calculating ϕ are statistically meaningful. Table 2 provides a practical example of the use of this method on the relevés of the different TSY included in this article.

Phi-coefficient values were calculated using the program JUICE 7.0 (www.sci.muni.cz/botany/juice.htm), which, besides estimating other statistical measures useful for the analysis of plant communities (*cf*. Tichý, 2002a), is also a powerful tool for ordering tables containing data for any number of relevés and to obtain conventional frequency synoptic tables when only absence/presence data are introduced, or mean frequency or cover tables, when working with cover or abundance-dominance data.

2.2 The Ochiai Index (*OI*)

Following the first proposal of the use of the phi-coefficient, a series of works of its practical application ensued (Cerná & Chytrý, 2005; Knollová, Chytrý, Tichy, & Hajek, 2005; Koci et al., 2003; Petrík & Bruelheide, 2006). These studies described the method as extremely useful for identifying mutual fidelity but, owing to its independence of the context, it could not be employed to detect differential species, given that these by definition are dependent on the setting. Moreover, for large data sets, the phi-coefficient can be affected to the extent that its statistical power is low.

When N increases, the number of species deemed significantly diagnostic will naturally increase, although this does not necessary imply changes in ϕ-values. Phytosociological data sets contain many different vegetation types. Thus, when N increases, the ecological context of the data set broadens and the frequency of almost all the species diminishes. Indeed, when dealing with large data sets of increasing ecological range, the n-value of any given species will eventually stop growing. Even at this point, however, more relevé data could still be added. The Φ-values obtained would increase for all species, because adding double zeros increases the correlation between two binary variables (De Cáceres et al., 2008).

For large data sets, when N tends towards infinity, this statistical distortion is avoided using *OI*, an index first used by Ochiai (1957) in a study on fish populations off the Asian Pacific coast and then used by Janson and Vegelius (1981) in other ecological association studies:

$$OI = \sqrt{\frac{n_p^2}{n \cdot N_p}}$$

Since the Ochiai index is independent of N, it is a measure of mutual fidelity between a given taxon and the TSY that excludes those relevés not belonging to the TSY. If its two components are, however, separated, the first is a measure of constancy, an indicator of the asymmetrical fidelity of the TSY to the species (Juhász-Nagy's asymmetric fidelity type 1), and the second is an asymmetrical measure of fidelity type 2, i.e., of the species to the TSY. An additional value of the *OI* is its close relationship with an index that assesses the indicator role of the species, *IndVal,* which is much used in ecological studies (De Cáceres & Legendre, 2009).

De Cáceres et al. (2008) proposed an alternative method for statistical measures that basically consists of two measures: the phi-coefficient to find the differential species (thus inverting its original intention) and *OI*, used both integrally and decomposing it into both components to search out the regional diagnostic species (Table 1). The setting of the region would obviously vary according to the reference sample from which the relevés arose.

The aim of the present study was to promote methodological standardization in syntaxonomy by stressing two main points: the need to explicitly distinguish between the procedures involved in the definition of syntaxa, and the need to support and improve the syntaxa defined using statistical measures of fidelity, a process included within the broad concept of "consistency in assignment" (De Cáceres & Wiser, 2011). With such an objective in mind, we here assess the efficacy of the four fidelity measures provided in Table 1, using as TSY communities whose syntaxonomical scheme has been established by us in earlier works (Peinado, Aguirre, Delgadillo, & Macías, 2008; Peinado, Ocaña-Peinado, Aguirre, Delgadillo, & Díaz Santiago, 2011; Peinado, Aguirre, Macías, & Delgadillo, 2011). Owing to their peculiar floristic composition and restricted geographical distribution these target syntaxa are a useful test of how such measures vary according to both the geographical and ecological context.

3. Material and Methods

3.1 Data Sets

The data for the TSY, comprising 224 relevés belonging to the class *Atriplici julaceae-Frankenietea palmer*, are provided in Table 2. The endemic assemblage of the communities of this class is remarkably high (Peinado et al., 2008, 2011a). This makes these data highly representative for a comparative analysis within its own internal context to detect differential species, and for stepwise ever-wider range comparisons both in the geographic and ecological context to detect diagnostic species.

The whole data set was obtained by combining three successive partial data sets that step-by-step expanded the geographical and ecological contexts with respect to the TSY. The first partial data set was prepared by combining the data for TSY with REF-1, comprising 252 relevés from other coastal communities of Baja California. The second partial data set combined the relevés in the first partial data set with a second reference group (REF-2), and comprised the 724 relevés taken of beach and dune vegetation along the Pacific coast from California to Alaska. Thus, the groups REF-1 and REF-2 include a total de 976 relevés of psammophilous communities taken from the southern tip of Baja California to Cook Inlet, Alaska. Within the third reference group (REF-3), were included 418 relevés related to successional stages of dune forests of the North American Pacific coast. Lastly, within the fourth reference group (REF-4), we included 3461 relevés obtained in all types of communities in western North America, 2909 of which were obtained from the literature and a further 552 from our own unpublished relevés. Thus, the entire data set was comprised of 5092 relevés encompassing 2620 vascular taxa. Although for all the relevés, original data were Braun-Blanquet abundance/dominance data, these were all transformed to presence (1) or absence (0) data.

Table 2. Syntaxonomy, codes and number of relevés of the target syntaxa

	Associations	1	2	3	4	5	6	7	8	9	10	11	12	*Np*	*s*	*N'p*
O-1	**Frankenietalia palmeri**													101	0.3	51
Al-1	**Atriplici julaceae-Frankenion palmeri**															
	Atriplex julacea		81	88	90		25	52	62		42	36	100			
	Frankenia palmeri	100	100	100	43			19		29	33		24			
	Lycium californicum		28	61	100		13				17					
	Euphorbia misera		16	100	52											
	Suaeda taxifolia				33		13					14				
As-1	**Atriplici linearis-Frankenietum palmeri**													15	0.3	3.8
	Atriplex s. *linearis*	100														
As-2	**Atriplici julaceae-Frankenietum palmeri**													32	0.3	8
As-3	**Euphorbio miserae-Lycietum californici**													33	0.3	8.3
As-4	**Dudleyo cultratae-Lycietum californici**													21	0.3	5.3
	Dudleya cultrata				90		25	33								
	Mirabilis v. *californica*				38											
O-2	**Camissonio crassifoliae-Isocometalia menziesii**													123	0.5	62
Al-2	**Heliantho nivei-Isocomion menziesii**													55	0.3	18
	Camissonia crassifolia					85	13	57		80	75		24			
	Isocoma v. *menziesii*					100	13	62	54			36	14			
	Atriplex s. *canescens*						50	10		25	17	45	19			
	Helianthus s. *niveus*						75	90	85			27				
	Ephedra californica					14	25	33				100				
	Cynanchum peninsulare					54	13				25	18				
	Distichlis spicata						38						14			
	Lotus distichus						25	33								
	Camissonia s. *suffruticosa*						38	19								
	Lotus rigidus						25	10								
	Carpobrotus chilensis						25		46							
As-5	**Loto bryanthii-Isocometum menziesii**													13	0.3	3.3
	Lotus bryantii				85											
	Amaranthus watsonii				85											

Code	Syntaxon										Np	s	N'p
	Dalea brandegeei		31										
As-6	**Heliantho nivei-Isocometum vernonioidis**										8	0.3	2
	Isocoma v. *vernonioides*			100									
As-7	**Camissonio crassifoliae-Helianthetum nivei**										21	0.3	3.3
As-8	**Heliantho nivei-Astragaletum anemophili**										13	0.3	3.3
	Astragalus anemophilus					100							
Al-3	**Encelion ventori**										36	0.3	12
As-9	**Camissonio crassifoliae-Encelietum ventori**										24	0.5	12
As-10	**Sphaeralceo fulvae-Encelietum ventori**										12	0.5	6
	Encelia ventorum						100	75					
	Sphaeralcea fulva							100					
Al-4	**Lycion richii**										32	0.3	11
As-11	**Ephedro californicae-Lycietum richii**										21	0.5	11
As-12	**Lycietum brevipedis**										11	0.5	5.5
	Lycium richii	19		38	10		17	25	100	100			

The first 12 columns show the syntaxonomical scheme of the class *Atriplici julaceae-Frankenietea palmeri* summarized from Table S-10 in Peinado et al. (2011a). Scores are presence percentages (rounded) for each association. The last three columns indicate: *Np*, number of relevés belonging to each target syntaxon; *s*, standardization factor for syntaxa of varying size belonging to the same syntaxonomical hierarchical level; *N'p*, number of standardized relevés after multiplying *Np* by *s*. The following abbreviations are used in tables 2, 3 and 4: *Atriplex canescens* subsp. *canescens* (*Atriplex* s. *canescens*), *Atriplex canescens* subsp. *linearis* (*Atriplex* s. *linearis*), *Camissonia cheiranthifolia* subsp. *suffruticosa* (*Camissonia* s. *suffruticosa*), *Helianthus niveus* subsp. *niveus* (*Helianthus* s. *niveus*), *Isocoma menziesii* var. *menziesii* (*Isocoma* v. *menziesii*), *Isocoma menziesii* var. *vernonioides* (*Isocoma* v. *vernonioides*), *Mirabilis californica* var. *californica* (*Mirabilis* v. *californica*).

3.2 Stage 1: Internal Analysis of Fidelity and Differential Species

To evaluate the results obtained in the syntaxonomic classification undertaken using the floristic-sociological approach combined with cluster analysis (*cf*. Peinado et al., 2008, 2011a, 2002b), whose results we summarize in Table 2, in this initial stage, we estimated measures of fidelity (ϕ coefficient) within the class by comparing: a) orders against orders; b) alliances against alliances within the same order and; c) associations against associations within the same alliance. The fidelity analysis was not applied to the association *Atriplici julaceae-Frankenietum palmeri,* because this association is the "central association" of the class, which is primarily defined according to the absence of positive diagnostic species (Dierschke, 1988).

Taking into account the different sizes of the TSY, to calculate the phi-coefficient these were all equalized applying factor *s* to the syntaxa compared (Table 2). For the statistical basis of this factor, the reader is referred to Tichý and Chytrý (2006). Confidence intervals for Phi-values were established using Fisher's *z* transformation. To estimate the standard deviation, Fieller and Pearson (1961) correction was used. The program JUICE 7.0 was used to calculate the phi-coefficient.

3.2 Stages 2, 3, 4 and 5: Identifying Diagnostic Species

OI was calculated to identify the diagnostic species of the class and to monitor changes in this index in four successive scenarios that each time extended the ecological and geographic context. This was done by detecting changes in the values of *OI, c* and *p* appearing in Table 1. Comparisons were made by considering each TSY versus the set of REF corresponding to each stage:

> Stage 2: TSY versus REF-1.
>
> Stage 3: TSY versus REF-1 + REF-2.
>
> Stage 4: TSY versus REF-1 + REF-2 + REF-3.
>
> Stage 5: TSY versus REF-1 + REF-2 + REF-3 + REF-4.

Since *OI* is independent of the relative number of relevés within groups, no measure of standardization was applied. For the confidence intervals of *OI*, the asymptotic approximation of the variance proposed by Janson and Vegelius (1981) was used.

Plant nomenclature follows Wiggins (1980), except for *Helianthus* (Heiser, Smith, Clevenger, & Martin, 1966) and *Isocoma* (Nesom, 1991).

Table 3. Results of the analysis of fidelity within the class *Atriplici julaceae-Frankenietea palmeri*. Syntaxa codes as in Table 2. *Φ*, phi-coefficient of association. UL and LL, upper and lower limits, respectively, of the confidence intervals (95%) for *Φ*. All values are multiplied by 1000 and rounded. Only species with *Φ*-values > 400 are shown

	LL	*ϕ*	UL
O-1			
Frankenia palmeri	643	715	775
Euphorbia misera	426	530	620
Lycium californicum	407	513	605
O-2			
Isocoma v. *menziesii*	313	429	532
Helianthus s. *niveus*	288	406	512
Al-2			
Helianthus s. *niveus*	510	632	729
Isocoma v. *menziesii*	402	543	659
Al-3			
Encelia ventorum	916	941	959
Camissonia crassifolia	678	765	831
Sphaeralcea fulva	288	445	579
Al-4			
Lycium richii	699	781	843
As- 1			
Atriplex s. *linearis*		1000	
As-3			
Euphorbia misera	350	486	602
Fouquieria diguetii	301	443	566
Errazurizia benthamii	269	415	542
As-4			
Dudleya cultrata	424	550	655
Lycium californicum	362	497	611
Pachycereus schottii	331	470	589
Mirabilis v. *californica*	293	436	560
Isocoma v. *menziesii*	313	429	532
Helianthus s. *niveus*	288	406	512
As-5			
Lotus bryantii	842	884	915
Isocoma v. *menziesii*	418	545	651
Proboscidea althaefolia	415	542	649
Cynanchum peninsulare	313	454	575

	LL	ϕ	UL
As-6			
Isocoma v. *menziesii*	859	897	925
Distichlis spicata	351	487	603
Abronia maritima	346	483	600
Camissonia s. *suffruticosa*	269	415	542
Helianthus s. *niveus*	253	401	530
As-7			
Helianthus s. *niveus*	455	576	676
Lotus distichus	302	444	567
As-8			
Astragalus anemophilus	960	971	979
Carpobrotus chilensis	395	525	635
Helianthus s. *niveus*	347	484	601
As-9			
Camissonia crassifolia		1000	
Encelia ventorum	702	777	835
Haplopappus sonorensis	289	433	558
As-10			
Sphaeralcea fulva	923	944	959
Encelia ventorum	324	464	584
As-11			
Lycium richii	451	573	674
As-12			
Ephedra californica	499	613	706
Lycium richii	384	516	627

4. Results

Table 3 provides the results of the internal analysis of fidelity of the class *Atriplici julaceae-Frankenietea palmeri*. Table 4 shows the values of *OI,* constancy and frequency for the ten species showing the highest values and that may be considered diagnostic of the class. This table summarizes the changes produced in *OI* in the stages 2 to 5. These changes are illustrated in Figure 1.

5. Discussion

If the frequencies provided in Table 2 are compared with the values of *Φ* appearing in Table 3, it may be clearly seen that the latter confirm the syntaxonomic classification based on classic phytosociological methods backed by clustering methods. However, using phi-coefficients some differential species were detected that had been overlooked by the previous analyses due to the size of the data set (1730 relevés). Such are the cases of *Fouquieria diguetii* and *Errazurizia benthamii,* differential species in association As-3*,* of *Pachycereus schottii* in As-4, of *Distichlis spicata* and *Abronia maritima* in AS-6, and of *Haplopappus sonorensis* in AS-9.

The results of the internal fidelity analysis reveal that the more heterogeneous a syntaxon is, the lower are the phi-coefficient values of association. Thus, when the two orders are compared, the *Φ*-values for the two differential species of the order O-2, are lower than those corresponding to the differential species of O-1, despite both species being exclusive to the order (Table 2). In contrast, the phi-coefficient of *Frankenia palmeri* is almost double that of the differential species of order O-2, despite the fact that it appears in some associations of this last order. The increased heterogeneity as the cause of the decline in the phi-coefficient also emerges when we compare the three alliances of O-2. Thus, the coefficients of the differential species of alliance Al-2,

which contains four associations, are much lower than those of alliances Al-3 and Al-4, each of which encompasses two associations.

The internal heterogeneity of a given syntaxon gives rise to marked drops in the Φ-values of those plants that, although being practically character species of this syntaxon, are absent from some of its components. Such is the case of *Euphorbia misera* in the order O-1, despite not appearing in O-2. However, its absence from the association As-1, comprised solely of two plants owing to its extreme habitat, is the cause of its relatively low ϕ-coefficient.

The use of the phi-coefficient alone to confirm the differential value of a particular taxon is almost absolute in cases of highly delimited ecological or geographical contexts. With regard to the ecological context, this is the case of *Atriplex canescens* subsp. *linearis* in As-1 and of *Isocoma menziesii* var. *vernonioides* in As-6, given they both prosper in soils moistened by brackish water, a different habitat to the rest of the communities of the class. Both species have a wide distribution area, but they grow in settings ecologically differentiated from those of the remaining associations of their own alliance. The geographic context is apparent for the associations characterized by a microendemism, such as in the case of *Astragalus anemophilus* (As-8), *Lotus bryanthii* (As-5), *Camissonia crassifoli*a (As-9) and *Sphaeralcea fulva* (As-10). The fact that some of these species fail to attain a fidelity value of 1 can be attributed to their occasional presence in zones of contact with neighbouring associations or, in the case of *L. bryanthii,* to its absence in one relevé of As-5.

When the Φ-values are not so high, the differential role of certain species is reinforced by combining these data with the frequency data. Such are the cases of *Isocoma menziesii* var. *menziesii* and *Helianthus niveus* subsp. *niveus* in the order O-2. Their fidelity values are not relatively very high due to the heterogeneity of the order, which has three alliances. If we examine the frequencies of these two species in Table 2, it becomes clear that they never occur in the communities of the order O-1, such that their fidelity is negative with respect to the latter.

Table 4. Search results for diagnostic species in the four successive stages examined (see methods for details). *Np*, number of relevés in each partial data set; *n*, number of species appearances in each partial data set; c, constancy (*np/Np*), where *np* is the number of species appearances in the TSY; *f*, frequency (*np/n*); *OI*, Ochiai index. LL and UL, lower and upper limits, respectively, of the confidence intervals (95%) for *OI*. Values multiplied by 1000 and rounde

| Stages	2	3	4	5	2	3	4	5	2	3	4	5		2			3			4			5	
Np	489	1213	1631	5092	489	1213	1631	5092	489	1213	1631	5092		489			1213			1631			5092	
	n	*n*	*n*	*n*	*c*	*c*	*c*	*c*	*f*	*f*	*f*	*f*	LL	*OI*	UL	LL	*OI*	UL	LL	*OI*	UL	LL	*OI*	UL
Atriplex julacea	144	144	144	150	0.6	0.6	0.6	0.6	0.9	0.93	0.93	0.89	728	746	764	735	746	757	737	746	756	730	731	742
Frankenia palmeri	116	116	116	121	0.5	0.49	0.49	0.49	0.9	0.94	0.94	0.9	658	676	695	665	676	687	667	676	686	661	662	673
Lycium californicum	69	69	69	91	0.3	0.25	0.25	0.25	0.8	0.81	0.81	0.62	432	450	469	439	450	462	441	450	460	391	392	403
Euphorbia misera	54	54	54	79	0.2	0.24	0.24	0.24	1	0.98	0.98	0.67	464	482	500	471	482	493	472	482	491	397	398	410
Lycium richii	51	51	51	52	0.2	0.22	0.22	0.22	1	0.98	0.98	0.96	449	468	486	457	468	479	458	468	477	462	463	474
Helianthus s. niveus	41	44	44	44	0.2	0.18	0.18	0.18	1	0.93	0.93	0.93	410	428	446	402	413	424	403	413	423	412	413	424
Isocoma v. menziesii	41	46	46	52	0.2	0.18	0.18	0.18	1	0.89	0.89	0.79	410	428	446	393	404	415	394	404	414	379	380	391
Encelia ventorum	34	34	34	34	0.2	0.15	0.15	0.15	1	1	1	1	371	390	408	378	390	401	380	390	399	388	390	401
Dudleya cultrata	29	29	29	29	0.1	0.13	0.13	0.13	1	1	1	1	342	360	378	349	360	371	350	360	369	358	360	371
Camissonia crassifolia	24	24	24	24	0.1	0.11	0.11	0.11	1	1	1	1	309	327	346	316	327	338	318	327	337	326	327	338
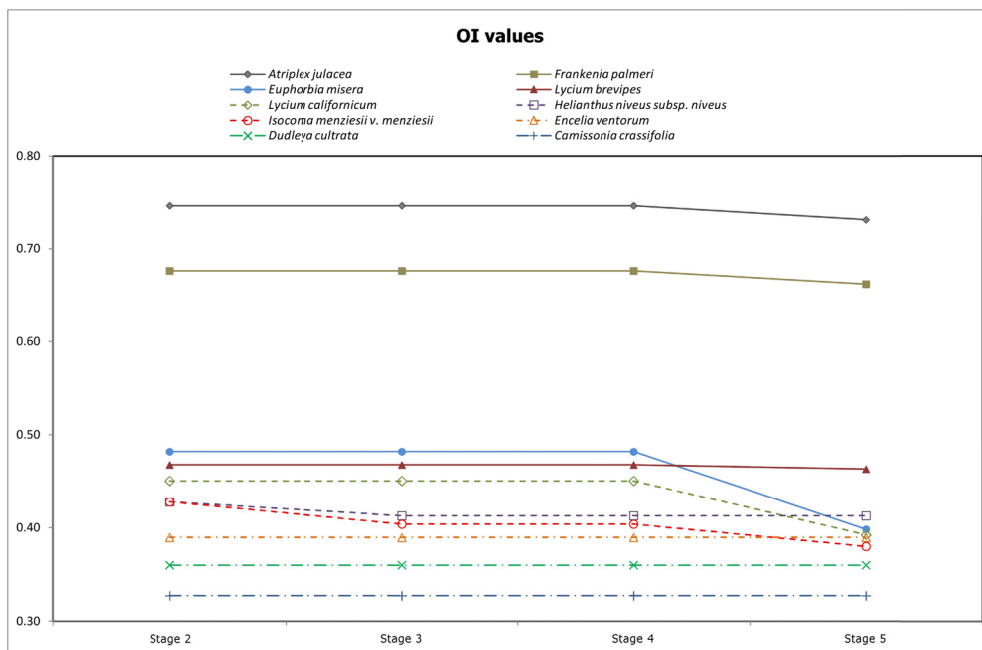
Figure 1. Ochiai index (OI) values recorded for the ten species showing the highest phi-coefficients in the successive stages of increasing the data set

Table 4 (represented in Figure 1) shows the ten species with the highest *OI* values, which are the diagnostics of the class *Atriplici julaceae-Frankenietea palmeri*. Values of asymmetric fidelity are as we would expect. Constancy (*c*) values are lower the more characteristic of a given syntaxon of inferior hierarchy to the class are the plants considered. The *p* value of asymmetric fidelity of a given species to a given syntaxon is highly significant. With the exception of *Lycium californicum,* the ten diagnostic species show values above 0.9 although some decrease considerably in Stage 5 for reasons that we discuss below.

It should be noted that in Stage 2, we included 265 relevés taken of coastal communities of Baja California that ecologically and geographically border with those of the class *Atriplici julaceae-Frankenietea palmeri*. On the Baja Californian coast, it is common to find rocks containing different proportions of sodium, which determines that the most frequent species in the class, *Atriplex julacea* and *Frankenia palmeri*, bioindicators of alkaline substrates, may sporadically appear in communities belonging to other classes. Due to this, both these species show the lowest *p* values among the 10 diagnostic species. In contrast, species of a more reduced ecological context, i.e., the character species of the order O-2 and of its three alliances, show *p* values of 100%.

In Figure 1, it may be seen that *OI* values remain practically constant as the number of relevés in the successive stages increases along with their geographic and ecological contexts. The following are, however, the exception. In the case of *A. julacea* and *F. palmeri*, a small decrease in the index occurs in Stage 5, since the 3461 relevés of REF-4 added in this stage include some taken along the Baja Californian coast that occasionally contain both plants. The drop in *OI* is most marked for *Lycium californicum* and *Euphorbia misera*, two more widely distributed species that appear in communities of the class *Prosopido torreyanae-Fouquieretea splendentis*, 247 of whose relevés were introduced in Stage 5.

The case of *Isocoma menziesii* var. *menziesii* is different to that of the rest of the diagnostic species because its *OI* goes down both in Stages 2 and 5. This is a strict psammophilous, whose distribution extends from Bahía Magdalena on the central Baja Californian coasts to central California. In Baja California it is an exclusive element of secondary dunes and, as such, a species regionally characteristic of the order O-2. Its distribution in California is wider and it inhabits both coastal sands within communities of the class *Ambrosietea chamissonis* (Peinado et al., 2011a) and interior zones (USDA, 2011). Its *OI* drops in Stage 2, when the 522 relevés of *Ambrosietea chamissonis* are incorporated and slightly drops again in Stage 5 for the same reasons described above for *L. californicum* and *E. misera*.

6. Conclusions

The use of fidelity measures supports and improves the results of phytosociological classification based on comparing more or less numerous sets of relevés that are, nevertheless, always limited by the ecological and geographical contexts. If we use as reference groups data sets with many relevés, both these contexts will be expanded with the consequence of the increased diagnostic and bioindicator value of a given species. With the recent introduction of large phytosociological databases, it should be possible to preferentially identify diagnostic species of more general validity in data sets that include relevés of most vegetation types occurring across a wide area.

In phytosociological and syntaxonomical practice, the diagnostic value of a species is established using standardized phytosociological methods (comparisons among relevés, table rearrangements, and expert knowledge) supported by numerical methods that lead to a final syntaxonomic classification. Once these syntaxonomic hierarchies have been defined, their diagnostic value as abstract vegetation units and the bioindicator values of their species can be reinforced using the two measures of mutual fidelity analysed here: the phi coefficient and Ochiai index.

The phi-coefficient is dependent on the context and can therefore be used to assess fidelity in previously classified vegetation units with the aim to evaluate the fidelity of the differential species in the syntaxa being compared.

The *OI* is a measure of fidelity that excludes "double zeros" or "double absences". In other words, when the size of the reference data set is increased by incorporating relevés lacking any TSY species, its value remains unchanged. Thus, since *OI* is independent of the size of the TSY and of the whole data set, it is only affected by those relevés that contain the species for which this index is being calculated. As more relevés lacking a given reference species are added, the *OI* will not change, no matter how many relevés the TSY is compared with. However, independently of the size of the latter, when relevés that include species present in the TSY are added to the data set, this causes changes in the *OI*, such that this index is able to discriminate diagnostic species with more precision than the phi-coefficient.

The methods used to assess fidelity are not in themselves classification systems, but can be extraordinarily useful for three essential purposes: a) to *a posteriori* check and improve a classification undertaken using classic phytosociological methods by identifying highly statistically significant diagnostic species independently of the context. This is very useful both in Europe, where the phytosociological approach has given rise to very complete syntaxonomical schemes, and in other world zones with scarce phytosociological tradition but that have available data from surveys conducted through other methods compatible with these new approaches; b) to detect species with high fidelity values in groups of relevés classified or ordered according to ecological or phytogeographical factors when data sets for many relevés are included, a task that is extremely cumbersome or impossible using intuitive or deductive traditional classification methods; and c) to use the taxa returning higher fidelity values as ecological or biogeographical indicators.

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