



Point of view

Convex hulls, habitat filtering, and functional diversity: mathematical elegance versus ecological interpretability

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Abstract: There is a recent proposal to apply convex hulls to the measurement of habitat filtering, trophic diversity and functional richness. Although this approach has successful applications, some conceptual difficulties with the interpretation of results should not be overlooked. The basic assumption that trait convergence and the associated deflation of the convex hull is a result of environmental (habitat) filtering does not always hold, because 1) some traits may converge as a result of competition as well, and 2) environmental factors, such as disturbance, may lead to divergence, rather than convergence for certain characters. There is neither evidence nor theoretical proof that increasing correlations between traits and reduction in trait combinations are always caused by habitat filtering, especially when individual trait ranges are unchanged. Diversity measurements in terms of convex hull volumes may be misleading because zero or near zero values may result no matter how wide the individual trait ranges are. For these reasons, applications of convex hulls cannot be viewed uncritically, and considerable care must be taken even if the method is used in combination with other techniques.

Introduction

There is a general view suggesting that two fundamental processes, competition (e.g., plant-to-plant interaction) and habitat (i.e., environmental) filtering can be considered as major processes underlying community development (Diamond 1975). Most ecologists agree that these processes are more faithfully reflected by morphological and functional traits than by the taxonomic relationships among component species. A classical hypothesis claims—or rather two complementary theories suggest—that competition and habitat filtering manifest themselves in the opposite manner during community assembly: strong species interactions increase divergence in functional traits (niche differentiation) whereas substantial habitat filtering effects lead to the convergence of traits (see e.g., Kraft et al. 2008 and references therein). Accordingly, there should be competition-driven communities in which environmental conditions are favourable for a wide variety of plant strategies, as opposed to environment-constrained assemblages to which habitat filtering may be several magnitudes more influential than biotic interactions. Between these endpoints, there is an evident continuum of intermediate stages in which both processes operate simultaneously (Weiher et al. 1998). A practical problem is thus to express quantitatively the departure of a given species assemblage from the neutral case in either direction, to test this departure statistically and to identify traits that are mostly responsible for non-randomness. Recently, a

mathematical construct from computational geometry, the convex hull (Fig. 1a) has been advocated by Cornwell et al. (2006) to measure deviation from null model situations in the multidimensional trait space. Those authors suggested that deflation of convex hulls is the manifestation of habitat filtering and proposed the volume change as a test statistic. Encouraged by the mathematical elegance of the procedure, Layman et al. (2007) went further by measuring trophic diversity in food webs based on the volume of convex hulls, while Villéger et al. (2008) described a similar method to quantify functional richness of communities. However, I argue that the convex hulls do not necessarily express background processes in a way the proponents of their use intend to demonstrate. This paper first lists two groups of difficulties with this approach as applied to measuring habitat filtering effects: one is ecological and the other mathematical. Hypothetical examples demonstrate that competition may cause both inflation and deflation of convex hulls in the trait space and therefore its distinction from habitat filtering effects is equivocal. Also, there may be cases such that the individual trait ranges are unchanged—reflecting the situation that the environment did not act upon extreme traits—but the convex hull is changed in volume. Interpretation is also problematic because by the convex hull one attempts implicitly to capture two different things, the dispersion of species in trait spaces and its change simultaneously. In the second part of the paper, I explain why the difficulties with the measurement of any component of diversity are more severe: the convex hull

is inappropriate for this purpose because of the ill-defined zero point.

Convex hulls and habitat filtering

After van der Valk (1981), Keddy (1982) and several other authors, Cornwell et al. (2006) refer to habitat filtering as “a reduction in the range of successful strategies among coexisting species” due to the environment. In statistics, range corresponds unambiguously to the difference between the maximum and minimum of a given variable in the sample (Sokal and Rohlf 1981). A multivariate generalization of range is the smallest hyperrectangle that contains all points (see e.g., Bentley and Friedman 1979), which is determined by the minimum and the maximum along each dimension of the multidimensional space. This mathematical object has long been known in niche theory (May 1974, Feoli et al. 1991). Its volume is obtained as the product of the ranges on individual trait dimensions. Alternatively, the sum of range values may be used to avoid zero volume if a given trait happens to be constant.

If we wish to be consistent with the rigorous statistical definition of range, then the effect of habitat filtering should be measured by the volume or range sum changes of the hyperrectangle resulting from the exclusion of species with extreme trait features that reflect extreme ecological requirements. However, Cornwell et al. (2006) extend the meaning of the term range—somewhat arbitrarily—to the *convex hull*, i.e., the smallest convex polyhedron (or polytope, Büeler et al. 2000) that encloses the points representing the species, thus interpreting any reduction in the volume of the convex hull as the manifestation of habitat filtering.

Pros and cons

The main argument in favour of using a convex hull is that it is usually a small portion of the hyperrectangle; as Cornwell et al. (2006) put it, “it reduces the amount of empty space compared to cubes”. No doubt that the convex hull volume gives in general a closer approximation to the trait space occupied by a community than the hypervolume—thanks to its smaller sensitivity to unoccupied parts of the hyperrectangle, the so-called “missing corners”. These missing corners—and the nearly triangular shape of the point cloud (in two dimensions)—result from the fact that certain combinations of trait values are impossible or unlikely (for example, large seeds combined with small leaves for woody species, as demonstrated by Cornelissen 1999; or small adult plant mass with large seed mass, Aarssen 2005). Quite appreciably, appearance of missing corners is attributed by Cornelissen to the complex interactions of three groups of factors, i.e., *ecological*, *phylogenetic* and *allometric* constraints. Then, the natural question arises: if the deviation of a convex hull from the corresponding hyperrectangle cannot be traced back

to a single phenomenon, can we nevertheless give a simple explanation of the deviation of one convex hull from another? Cornwell et al.’s (2006) answer is yes: they assume that the *volume difference* between the convex hull for a random selection of species and another for the species of an actual community is due only to habitat filtering. Whereas this may be true in several cases, I argue that some conceptual problems should not be neglected before one decides to adapt the method to any study of community assembly.

1. *Convex hull changes under constant habitat conditions.* Consider the set of four hypothetical examples in Fig. 1 which illustrate the problem in two dimensions, for simplicity, but without losing generality. In Fig. 1a, the species are positioned so as to give a relatively high convex hull area. In Fig. 1b–d, the actual minimum and maximum do not change which means that the habitat does not “filter out” any species with traits reflecting extreme ecological requirements. While the manifested minima and maxima in trait values remain the same, the convex hull decreases in area from b to d. Ultimately, all points fall onto a line and the convex hull collapses into a zero area (Fig. 1d)¹. Again, this set of examples have a non-trivial relationship with the habitat conditions because the ranges of trait values supported (or allowed) by the environment are unchanged. Although it has been shown that habitat filtering may act upon combinations of traits (e.g., Pausas and Verdú 2008), there is neither empirical evidence nor theoretical proof that changing correlations and altered trait combinations are *always* due to habitat filtering effects, especially when the ranges of traits remain the same. Cornwell et al. (2006) also recognize this uncertainty by admitting that “we *hypothesize* that specific combinations of ... functional traits that will not be viable in each habitat, leading to a reduction in the multivariate range at a given site”.

2. *Competition and the deflation/inflation of convex hulls.* The above hypothesis can be expanded by some other equally plausible explanations. For example, we can imagine a situation in which an extremely strong competitive pressure does not allow coexisting species to have identical trait values (at x and y in Fig. 2a), leading to trait shifts (arrows), increased correlations, and in turn to a reduced convex hull area (Fig. 2a). In other words, competition may increase the number of trait combinations (niche differentiation), therefore the number of viable strategies as well, and still the convex hull deflates. The reverse process is also possible, of course, because equal trait values (at x and y in Fig. 2b) can also be eliminated by a move in the opposite direction, as shown by arrows in Fig. 2b. In this case, competition has the supposed effect: the increasing number of trait combinations is associated with the inflation of the convex hull. The relationship between convex hull volume and the number of functional strategies is thus equivocal.

3. *Convergence versus divergence.* Convergence of traits and the associated deflation of the convex hull cannot always be

¹ The convex hull also has zero volume in the multidimensional space if there is a trait with the same value for all species. These constant traits can be identified and removed easily.

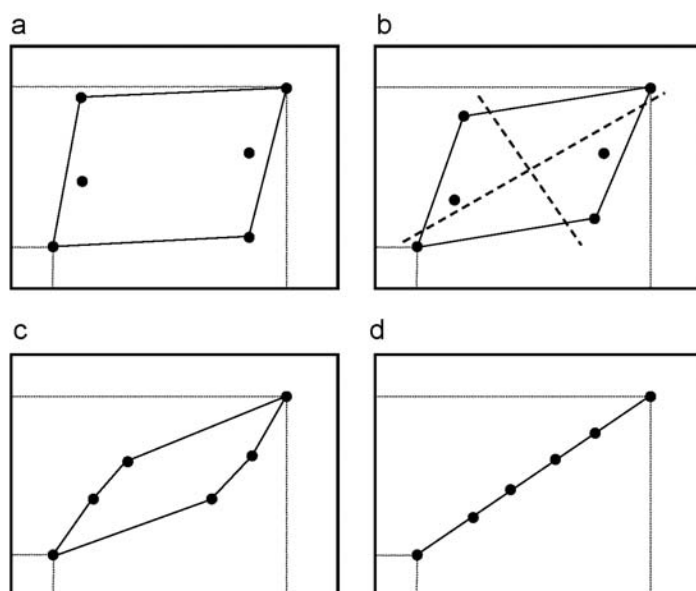


Figure 1. Convex hulls for six species (full symbols) in an hypothetical two-dimensional trait space. Area decreases along with increasing correlations between the two traits (a-d). Dotted lines indicate the individual ranges of the two traits. In b, dashed lines show approximately the position of principal components I and II.

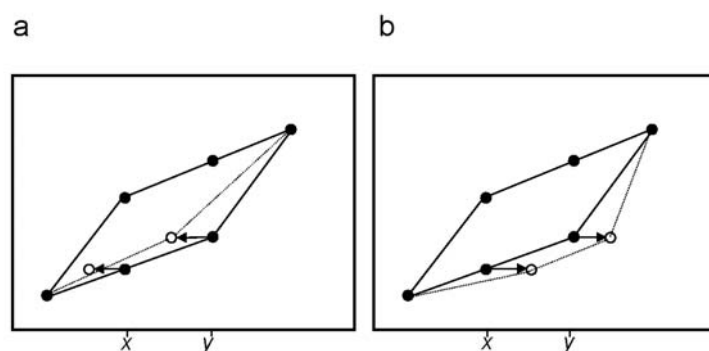


Figure 2. Examples illustrating that when competition (niche differentiation) increases the number of species strategies, the convex hull may either deflate (a) or inflate (b) in an hypothetical two-dimensional trait space. Arrows indicate trait shifts that cause new species positions (open circles), dotted line is the new border of the convex hull.

attributed to habitat filtering effects. As pointed out by Navas and Violle (2009), the so-called competitive effect traits (such as plant height) may also converge when competition is the dominant factor controlling plant fitness (productivity-related traits in Grime 2006). Furthermore, at the local scale disturbances (i.e., the environment) may enhance divergence, rather than convergence, for reproduction-related characters (Thompson et al. 1996). That is, whenever such traits are included in the study, the effect of habitat filtering and competition may be confounding, thus questioning direct ecological interpretation of any change in the conceptual trait space. This issue is subject to an ongoing debate on community assembly (see e.g., Grime 2006, Wilson 2007) whose conclusions cannot be ignored when any attempt is made to measure habitat filtering.

4. Convex hull volume, overall trait dissimilarity and their changes. After having examined some ecological aspects, let us see the mathematical properties of the convex hull-based method. Whereas the convex hull in Fig. 1d has a zero area, the species still have different strategies, albeit their dissimilarities are apparently lower than in Fig. 1a. Therefore, convex hull area (or hypervolume, in many dimensions) does not reflect properly the „range” of manifested trait combinations. An adequate expression of overall trait dissimilarity among species should take the minimum value, i.e., zero, only if all

species are identical for all traits. A mathematically more appropriate measure of the point scatter in the multivariate trait space is therefore not the volume, but perhaps the error sum of squares or average interpoint distances (Mason et al. 2003, Lepš et al. 2006).

The arithmetic difference between two volumes may also be misleading. Zero difference does not necessarily mean that the two convex hulls coincide; increases/decreases of trait correlations may be compensated for by expansion/compression of the individual trait ranges (Fig. 3). This peculiar relationship remains undetected if the convex hull volumes are calculated separately for the two assemblages and then subtracted from each other. We cannot predict how likely such situations are in actual studies and null model investigations, but it is an intriguing possibility that the interplay of trait correlation and range may lead to a zero volume change. A solution of this problem would be to measure the symmetric difference of the two convex hulls in question (dotted areas in Fig. 3), which is called the *template distance* (Veltkamp 2001), a measure readily generalized to many dimensions (with exponentially increasing computational difficulties, Bueler et al. 2000).

A fundamental mathematical problem with the convex hull approach is thus as follows. It tries to capture dispersion

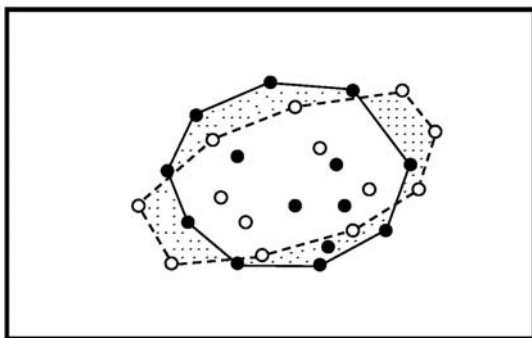


Figure 3. Hypothetical example showing two convex hulls with similar area but different range for one of the traits (horizontal axis) in a two dimensional trait space. Dotted areas indicate the symmetric difference between the two convex hulls (template distance). Full symbols: species in community 1, open symbols: species in community 2.

of species in trait spaces and its change simultaneously. However, multidimensional point scatter is reflected by sum of squares or average distances better than by volume and changes are shown by the template distance better than by absolute volume differences.

5. Unnecessary requirement of orthogonality. Cornwell et al. (2006) suggest more or less implicitly that their procedure performs optimally on orthogonal traits, thus avoiding highly correlated variables. In the illustrative example, they have chosen four traits that were not entirely orthogonal, with r ranging from 0.0 to 0.43. This suggests that, in practice, selection in favour of traits with reduced correlations is not straightforward; it is subjective without significance tests, and potentially ignores traits that may also be informative as to the measurement of habitat filtering. As Villéger et al. (2008) note: “any correlation between traits in the species-trait matrix may be considered a relevant aspect of species distribution in functional trait space”. There is no clear ecological reasoning to support complete elimination of correlated traits—that are otherwise relevant to habitat filtering studies—from the calculations. (It is not to say, of course, that studying trait relationships would be unnecessary by multivariate methods.) Furthermore, trait correlation structures may be different for the two communities being compared, and these are confounded if correlation is calculated for the pooled data. Cornwell et al.’s (2006) worries about lack of orthogonality are somewhat paradoxical: they prefer the convex hull because of its lower sensitivity to triangular shapes but triangularity almost always implies significantly non-zero correlation. (In Cornelissen’s study, $r = 0.51$ between seed size and leaf size.) For highly correlated traits, Cornwell et al.’s (2006) recipe is to use principal components analysis (PCA) first, followed by the computation of convex hull volumes in the component space. This does not help at all, because PCA does not influence the relative positions of points with the obvious consequence that the convex hulls do not change either (as illustrated by the two-dimensional example of Fig. 1b). The advantages of PCA therefore lie not in orthogonality *per se*, but rather in converting the data set to a re-

duced form which can then be processed effectively by the convex hull program whose performance greatly depends on the number of dimensions.

6. When the convex hull does not apply. What follows in this paragraph is not a critique of the convex hull approach, but rather a list of missing features showing its limitations. Having computed the volumes of convex hulls, either in the original trait space or along principal components, the traits mainly responsible for the changes cannot be identified. For a practical ecologist, however, it would be important to quantify the contribution of individual traits to any filtering effect. The convex hull based measure does not have an upper bound, which is not crucial in randomization tests, but values coming from different studies cannot be compared. The method is not applicable directly to situations when the number of points is equal to or less than the number of traits. The convex hull applies only to traits that are measured on the ratio and interval scale, i.e., to “quantitative” or “continuous” variables, while a vast amount of our present-day knowledge on the functional traits of species is carried by nominal and ordinal variables. Often, functional data bases contain many kinds of scale types simultaneously, which cannot be handled properly either. Finally, the convex hull method, at least its current implementation, does not tolerate missing values, while databases may be incomplete for several reasons (unavailable information, biologically undefined traits for certain species). These latter two problems can only be solved indirectly, by using the Gower formula (Gower 1971, Podani 1999) to compute between species dissimilarities and then performing a principal coordinates analysis to obtain ordination axes which can be used to calculate convex hulls.

Is there a solution?

Although for some time I played with the idea of developing a formula which resolves at least the mathematical difficulties, I think it is illusory to elaborate a perfect method for measuring habitat filtering effects unless we have some means to identify traits that are absolutely habitat related and independent of competition. We must be certain that any change in the trait space has to do with changes due to the habitat, and only with those changes, before attempting to measure the amount of that change. Separating the effect of convergent and divergent traits may represent a first step, as shown by Pillar et al. (2009) but this strategy has been developed for more than two communities arranged along a gradient.

Convex hulls and diversity

Layman et al. (2007) used two isotope ratios to define a two-dimensional space with the species of a trophic web as points. As a “proxy for the total extent of trophic diversity within a food web”, they also used—uncritically—the area of the convex hull drawn around the points. (This suggestion traces back quite clearly to the *TraitHull* web site of Schwillk and Cornwell, undated). If we consider Fig. 1a–d again, by redefining the axes to represent any functional variable, we

find that diversity decreases when the correlation between the two variables increases. For unit correlation, “diversity” defined in this way becomes zero which is counter-intuitive because the species still differ greatly in their trait scores. The same problem arises if one of the traits is constant. The fundamental criterion that diversity measures take the minimum value if and only if all elements of the collection are identical is thus violated². For similar reasons, the volume of convex hulls cannot be a meaningful measure of community level trait “variation” either (as suggested by Schamp et al. 2008) and is meaningless to express functional richness (as proposed by Villéger et al. 2008, despite my comments communicated to the authors). If we exclude the unit correlation case, as suggested by Villéger and co-authors, a near zero convex hull volume is still misleading when individual trait ranges are wide. We can end up with the paradoxical situation that functional richness (“the niche space filled by species in the community”) measured by Mason et al.’s (2005) method for individual traits is high, while the multivariate measure advocated by almost the same research team yields a very small value. It should be emphasized therefore that measures relying on areas or volumes are inappropriate to express *any kind of diversity or variation* and that convex hulls should not be used without examining the correlation structure in the trait space.

Is there a solution?

Measuring functional diversity does not involve the difficulty of separating competition and environmental effects, and thus the answer is definitely yes. The huge arsenal of functional diversity measures already available (see Petchey et al. 2004, Petchey and Gaston 2006, Ricotta 2005, Ricotta and Burrascano 2008, Schmera et al. 2009) should be scrutinized to find an appropriate measure of trophic diversity and another for functional richness. In any case, it is recommended to use several methods simultaneously because “their combination is likely to provide complementary information regarding the functional aspects of the community” (Brind’Amour et al. 2009). If the set of functional traits describing a food web includes a mixture of different scale types and some data are missing, situations that cannot be handled by the convex hull method, then the solutions suggested by Podani and Schmera (2006) are adequate for the measurement of trophic diversity. In particular, the average of all pair-wise Gower (1971) dissimilarities among species may be used to summarize species dispersion in trait spaces.

Concluding remarks

The convex hull is an attractive construct of computational geometry and is beneficial in several areas of ecology. In the estimation of home range of animals, the convex hull

approach has well-established practical utility (Worton 1995, Hatchwell et al. 2001), although the measurement of area may be biased (Burgman and Fox 2003). Further applications include the analysis of plant neighborhood relationships (Ellison et al. 1994), the visualization of overlap among groups of objects in two dimensional ordination scatter diagrams (Podani 2000) and the clarification of point configurations in ordinations (Gower and Hand 1996, Yee 2004), to mention only a few.

Although at first sight convex hulls appear superior to hyperrectangles in measuring the amount of community niche in trait spaces, one has to be extremely careful with interpreting their volume as expressing diversity or variation. Explaining *changes* of the convex hull volume in trait spaces is even more problematic, although there appear to be successful applications which cannot be objected (including Cornwell et al. 2006, Pausas and Verdú 2008). However, this paper argues that, contrary to the suggestions by Cornwell et al. (2006), there is no *single, universal* ecological/biological/mathematical explanation behind the difference between the volumes of two convex hulls. Environmental filtering and competition may act in a non-trivial and simultaneous way in forming the place of a community in the conceptual trait space. Hypothetical examples demonstrated that niche differentiation can manifest itself in two ways, either by deflation or by inflation of the convex hull. Trait divergence due to competition cannot be overemphasized because – depending on the traits used – competition may lead to convergence as well, thus making interpretation of convex hull changes difficult. The same is true for trait divergence which may result not only from competition but also from habitat effects on certain functional traits. Further discussion of the intricate subject of trait divergence and convergence in community assembly is beyond the scope of this short communication, the reader is referred to the vast literature of this subject matter (see Weiher et al. 1998, Grime 2006, Wilson 2007, Navas and Violle 2009, de Bello et al. 2009, and references therein). Zero deviation does not necessarily mean that the two convex hulls coincide and there are no changes in the range and multivariate intersection of traits. Therefore, the effect of any filtering process cannot be evaluated without examining the positions and shapes of convex hulls in the multivariate trait space.

Then, what are the perspectives for future research? I am sure that a new methodology is required to separate habitat filtering and competition at the trait level, as well as trait convergence and divergence (for the latter, Pillar et al. 2009 may be a good starting point). It is likely that the comparison of two communities is more meaningful with reference to a larger set of communities, preferably representing different stages along an ecological gradient. The measurement of functional diversity and richness, I feel, can do very well

2 For example, the Shannon diversity is zero only if the community is composed of a single species, and is positive in any other case. This is true for other diversity measures as well, except species richness for which the obvious minimum is 1. Furthermore, it should be pointed out that my comment is entirely independent of Hoetinghaus and Zeug (2008) whose criticism on Layman et al.’s (2007) paper concerns the use of isotopes as trophic traits.

without convex hulls, because a plethora of methods are available already.

Ecologists are often fascinated by complex mathematical objects, for instance, ordinations, dendrograms and other graphical structures; and convex hulls – as we have seen – are no exception. In my opinion, however, mathematical tools cannot resolve ecological problems without careful thoughts given to their advantages, disadvantages and potential pitfalls associated with their applications. This is especially true in highly disputed or fashionable areas of numerical community ecology, such as the measurement of habitat filtering, trophic/functional richness and diversity.

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