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The spatial organization of plant communities in a deciduous forest : A computational-geometry-based analysis

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Abstract

The use of Voronoi tessellation and Delaunay triangulation in studying the organization of plant communities is described. Data on the species identity, diameter at breast height and position of over 1500 trees, from three approximately one hectare plots with low, medium and high tree densities, located in the deciduous forest of Mudmalai sanctuary, Tamil Nadu, Southern India, form the basis of this analysis. By defining the local neighbourhood in terms of the Delaunay neighbours, we have devised an objective and unambiguous measure of intra- and inter-specific associations. The distribution of the number of neighbours is seen to be relatively independent of the tree density. The area of the voronoi cell of a tree is seen to be significantly and positively correlated with its diameter, and the strength of the association seems to be density-dependent. Other features such as the distribution of nearest-neighbour distances, the area–perimeter relationships, etc., have been analysed. The potential of this approach for the study of the long-term dynamics of plant communities is discussed.

Introduction

The various natural vegetation types such as forests, savannas and scrublands harbour a large number of plant species characteristic to them. However, the actual species composition observed at a particular location is dependent on the complex interplay of chance and evolutionary history. Thus, the mixed deciduous forests in the peninsular India contain about 250 tree species. Of these, about 150 are seen in the Mudmalai Wildlife Sanctuary. A typical one hectare plot in such a forest contains about 30 species[1]. If chance factors have a dominant role, such 'assemblages' would be no different from a randomly picked collection of species, using a suitable 'null model'. On the other hand, if specific groups of species have co-evolved due to their positive, favourable interactions with each other, they will be found to co-occur quite often – more often, in fact, on the basis of chance alone[2,3]. This logic can be extended to the interaction of a species with itself; a strongly favourable interaction between individuals of the same species leads to pockets of high local abundance of that species.

Thus, the composition of natural plant communities is strongly influenced by the intra- and inter-specific affinities of their constituent species. These are generally reflected in the spatial distribution of the species. Some species show highly clumped distributions, others, random, and still others, uniform. Some species are found significantly more (or less) often close to other species. Such patterns are most often analysed using a quadrat-based sampling. From the abundance of a given species, recorded from many quadrats, the mean (m) and the variance (v) are computed. The v/m ratio is an indicator of aggregation; values much higher than unity indicate a highly clumped distribution. Low values of v/m ratio correspond to a uniform (overdispersed) pattern, while a random (poisson) distribution corresponds to values close to unity[4, 5]. Similar data (abundance in different quadrats) can be used to quantify the degree of association between two species; higher frequencies of co-occurrence imply a high positive association.

While these techniques have been useful and widespread, one of their limitations is the arbitrariness inherent in the choice of the quadrat size. In fact, different quadrat sizes used for the same set of trees can give markedly different values of the indices of clumpiness and association[4]. In one sense, this is as it should be, since the quadrat size corresponds to a specific spatial scale; and the distribution could be clumped at one spatial scale, and not at another, smaller one. It would be valuable, however, if a natural spatial scale could be extracted from the distribution itself. One such alternative approach is based on the computation of the nearest neighbour distances and related statistics[4]. The limitation of this method is the restricted sampling of the neighbourhood, if only the nearest neighbour is considered. It is of course possible (though tedious) to include the next nearest, next-to-next nearest... neighbours. However, the arbitrariness of the stopping rule (cut-off point) makes this approach not a very satisfactory one.

A more objective and unambiguous method, proposed in the present study, is based on Voronoi tessellation. While the geometrical concepts of Delaunay triangulations and Voronoi tessellations have been in use for decades, their use has been limited as the algorithms to carry out these constructions are complex and highly computation-intensive. However, the easy availability of high-speed personal computers and of high-quality software (distributed via the internet) has made these computations readily accessible to many.

In the following section, we describe briefly these geometrical concepts. This is followed by the description of the data used in the present study. We next propose the concept of local neighbourhood, and describe the related computations for obtaining measures of intra – and inter-specific associations. We also describe the frequency distribution of the areas of voronoi cells corresponding to individual trees, and their relationship with the number of neighbours, diameter, and the overall tree density. Finally, the potential of this approach for the study of the dynamics of plant communities is discussed.

Definitions, data and analysis

(1) Voronoi cells : Let $T1$, $T2$, Ti, ...Tn be the positions of trees in a plot, defined by their (x, y) co-ordinates. For Ti, the set of all the points in the plane which are closer to Ti than to any other Tj is called the Voronoi cell (or Thissen polygon, or Dirichlet set) of Ti. As seen from Fig. 1, the voronoi cells are generally convex polygons. In some sense, the voronoi cell of a tree defines the 'territory' of the tree[5, 6]. The edges of the polygons are sets of points which are equidistant from the two nearby trees, and the vertices are points which are equidistant from three nearby trees. Though it is possible to have points equidistant from more than three trees, such situations are rarely encountered in practice. It may be noticed that trees which are on the periphery will have voronoi cells which are 'open', and hence will have infinite areas.

(2) Delaunay triangulation: Two trees whose voronoi cells share an edge can be defined as neighbours. If instead of drawing the voronoi cells, lines are drawn so as to connect all the pairs of trees which are neighbours, the region is decomposed into a set of non-overlapping triangles (Fig. 2). This process is called the Delauney triangulation, and has been extensively used for spatial data analysis in a variety of fields[7, 8].

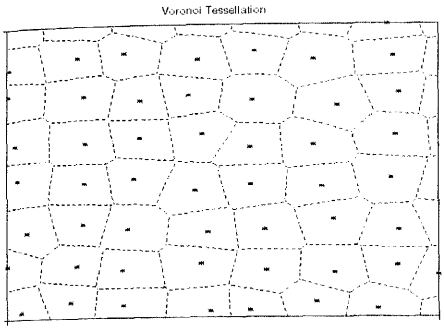

FIG. 1. Voronoi Tessellation of a set of points. The convex polygon surrounding each dot is a 'territory' of the dot in the sense that every point in the polygon is closer to that dot than to any other dot in the figure. Notice that the dot need not be at the center of its Voronoi polygon.

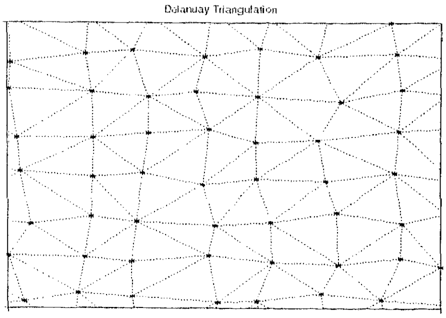

FIG. 2. Delaunay Triangulation for the set of dots of Fig.1, obtained by drawing lines joining those dots whose Voronoi polygons share an edge.

(3) Local neighbourhood: For every tree, we now define its local neighbourhood to be its voronoi cell. This appears reasonable since resources such as water and soil nutrients in the local neighbourhood will be by definition closer to this tree than to any other tree.

We also define local neighbours, or neighbour, of a tree as other trees whose local neighbourhoods are adjacent to its local neighbourhood. These are, in fact, the trees which are connected to it during Delanuey triangulation.

As seen from the above description, the definitions of neighbours and neighbourhoods are rigorous, objective, unambiguous and also biologically reasonable. In what follows, we describe the use of these notions in analysing the patterns of spatial distribution of trees.

(4) Data: The Center for Ecological Sciences has identified a 50 hectare plot, located in the deciduous forest of Mudmalai wildlife sanctuary of Tamil Nadu, Southern India, for a long-term study of forest dynamics. The 1000 m (east–west) by 500 m (north–south) plot has been surveyed and gridded to mark out parmanantly square quadrats 20 m to the side. All the trees with more than 1 cm DBH (diameter at breast height, *i.e.*, at a height 1.7 m from the ground) in the plot have been identified, and there spatial position recorded on a map to the nearest 10 cm. In 1988, the plot had over 26,000 individuals belonging to 72 species[7]. The survival and regeneration (new recruitment of individuals who have grown to be included in the 1 cm DBH class) has been recorded every year. The diameters of all the trees are remeasured and recorded every 4 years[9].

Since the information on the spatial location, species identity and the diameter for all the 25,000 individuals is computerized, it is easy to extact a subset with any desired characteristics. For the purpose of the present study, we have concentrated on three subplots approximately 1 hectare in size; one at the south–west corner, one at the center and the third close to the northern boundary of the plot. The choice was guided by the desire to sample plots of three different densities, and to place them reasonably far from each other.

(5) Software: The software required for Voronoi tessellation and Delauney triangulation was obtained from the ftp site of the Computational Geometry program of the University of Minnesota, USA (the program 'qhull') and from the netlib of AT and T (the program 'hull' developed by Dr.

Kenneth L. Clarkson, and the programs Triangle and Show Me developed by Dr. Jonathan Richard Shewchuk). Some of the statistical analysis was carried out using the program 'xldlas' written by Thor Sigvaldason (and downloaded from sunsite.unc.edu). All the computations were carried out on a 75 MHz pentium 75 MHz, running the Linux operating system (2.0.18).

(6) Computations: For each of the three plots, Delaunay triangulation and Voronoi tessellations were carried out. The points on the convex hull (periphery) were dropped. Further, all the points whose neighbours were on the periphery were also dropped, and only this smaller set of points was used for further analysis. This restriction had to be imposed since the areas of voronoi cells on the boundary are infinite – an artefact of ignoring trees beyond the boundary – and their inclusion would not have been meaningful.

The frequency distributions of the voronoi cell areas (VCA), nearest neighbour distances (NND), and number of Delaunay neighbours (which constitute the local neighbourhood of a tree) were obtained. Correlations between tree diameter, number of neighbours, nearest neighbour distance and voronoi cell area were calculated. The log–area versus log–perimeter relationships were also explored for voronoi cells as well as for delaunay triangles.

For every species, the proportion of individuals of the same species amongst all the local neighbours of all the individuals of that species was determined. A comparison of this proportion (using the chi-square test) with the proportion of individuals of that species found in the plot revealed the extent of clumpiness. A similar analysis for two different species indicated the degree of their association.

Results and discussion

1. *Degree of aggregation*

The three plots selected for the analysis eventually consisted of 194, 427 and 819 individuals and thus represented areas of low, medium and high tree density. Table I describes the statistical summary for the three plots (henceforth referred to as L, M and H plots). Though the mean area of voronoi cells increases as expected from H to M to L, it is interesting to note that the coefficient of variation is nearly the same for L and M, and noticably higher for the high-density plot. The distribution of voronoi cells (Fig. 3) is skewed to the right for the three plots, suggesting the presence of some rather large cells.

One of the measures of aggregation of the distribution of trees is the nearest-neighbour distance (NND); smaller values of NND would imply a more clumped distribution. The mean area of voronoi cells cannot directly be used as a measure of clumpiness, since it is simply the reciprocal of the density. The median, however, could be a possible indicator. A clumped distribution would produce a larger proportion of smaller voronoi cells, and shift the median to a value lower than the mean – a situation seen in all the three plots (Table I). Computing proportional departure of the median from the mean gives values of 0.12, 0.07 and 0.26, suggesting a high degree of clumpiness for the H plot.

Another indicator could be the coefficient of variation of voronoi cell areas, a larger value of the coefficient of variation corresponding to a more clumped distribution. As seen from Table I, even by this criterion, plot H is relatively more highly clumped. Interestingly, the coefficient of

Table I
Statistical summary of some of the parameters of the three plots with low (L), medium (M) and high (H) tree density. All the distances are in meters, and areas in square meters.

	Plot L	Plot M	Plot H
Density (#/Ha)	274.3	541.7	1013.2
No. of Trees	194	427	819
No. of Species	27	27	29
Voronoi Cell area			
Mean	36.46	18.46	9.87
Std. Dvn.	21.31	11.24	8.61
C. V.	0.584	0.609	0.872
Range	5.0–120.0	0.4–67.1	0.3–63.0
Median	32.1	17.2	7.3
No. of Neighbours			
Mean	5.9	5.9	5.9
Std. Dvn.	1.3	1.3	1.4
Range	3–9	3–10	3–13
Median	6	6	6
Nearest Neighbour Distance			
Mean	2.9	1.9	1.4
Std. Dvn.	1.5	1.3	1
C. V.	0.517	0.684	0.714
Range	0.4–7.7	0.2–7.5	0.1–6.2
Median	3	1.6	1.1

variation of the nearest-neighbour distances is low for plot L, and nearly equal for plots M and H, suggesting that NND and voronoi cell areas probe slightly different aspects of spatial distribution. In fact, the correslation coefficients between NND and voronoi cell areas are 0.67, 0.76 and 0.75 for the L, M and H plots. These are undoubtedly statistically highly significant values. However, in terms of the percentage of variance explained, these correspond to less than 60%, further confirming the slightly different features of spatial distribution as examined by NND and voronoi cell areas.

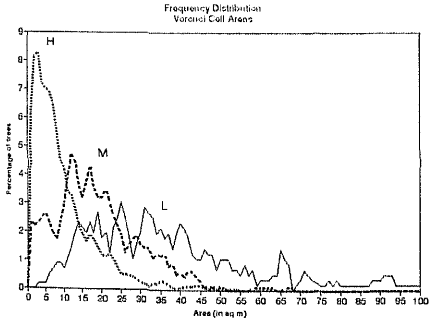

FIG. 3. Frequency distribution of the areas of Voronoi cells for the three plots corresponding to Low, Medium and High density of trees.

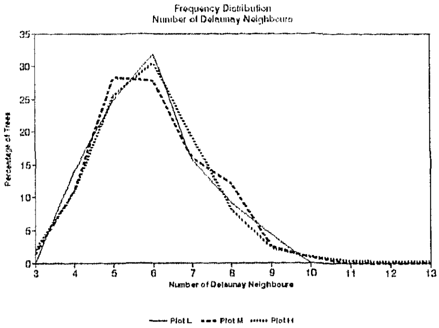

FIG. 4. Frequency distribution of the number of Delaunay neighbours for the three plots.

The indices suggested above serve mostly a descriptive purpose here. For statistical inference, however, it is necessary to compare these with those obtained under some appropriate null hypothesis, *e.g.* one that assumes a random (poisson) distribution of plants, or a negative binomial distribution with a prespecified value of contagion parameter. It is relatively straightforward to use Monte Carlo simulations to obtain the distribution of, say, C.V. of voronoi cells under any of these hypotheses, and compare them with the observed values. This has not been undertaken in the present study, however, and would form a part of future investigations.

2. *Local neighbourhood*

As seen from Table I, the mean number of (Delaunay) neighbours has nearly the same value (6) across the three plots despite their varying densities. This is not surprising, since for adequately large number of points in a plane, the mean is known to be around 6[6]. However, the constancy of the frequency distribution (Fig. 4) is rather remarkable.

Results of the regression analysis shown in Table II bring out the fact that the voronoi cell areas are highly and positively correlated with the diameter of the tree, and with the number of neighbours. The correlation between the latter two is, however, rather low, suggesting their nearly independent inflence. A multivariate regression involving both these as independent variables led to a multiple regression coefficient close to 0.60 for all the three plots. Quantitatively, an extra neighbour adds to the voronoi cell area to the same extent as an addition of 15–20 cm to the diameter.

Scatterplot of area vs diameter for plot L shown in Fig. 5 emphasizes the rather wide variation in the voronoi cell areas for trees having similar diameters. The positive correlation, however, is clearly discernible. A similar pattern is seen for plots M and H as well (data not shown).

It is possible that the voronoi cell area (VCA) is nonlinearly dependent on the diameter. In fact, a naive argument suggests the VCA to be proportional to the basal area, and thus to the square of

Table II.
Regression analysis for the three plots. Correlation and regression coefficients for the first two sections in the table (voronoi cell areas (sq. m.) vs diameter of the trees (cms), and vs the number of neighbours) are statistically highly significant. The last section reports the correlation between the number of neighbours and the diameter; all are marginally significant.

	Plot L	Plot M	Plot H
Area vs Diameter			
slope	0.46	0.21	0.26
intercept	24.5	15.1	6.6
corr. coeff.	0.379	0.266	0.378
Area vs # of neighbours			
slope	8.84	4.65	2.65
intercept	–15.9	–9.1	–5.9
corr. coeff.	0.55	0.558	0.422
Tree dia vs # neighbours			
corr. coeff.	0.21	0.074	0.088

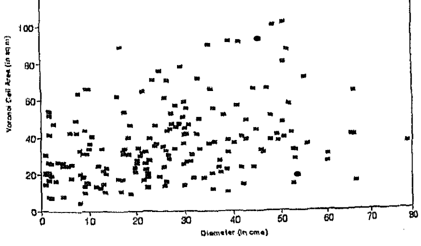

FIG. 5. Scatter diagram of the Voronoi cell area (y axis of a tree and the diameter (X axis) of the tree.

Table III

Statistically significant self-association for the species seen in the three plots. The columns indicate the plot, # of individuals, total # of neighbours, expected frequency of occurence (assuming the same proportion in the neighbours as in the plot), observed frequency of occurence, and the value of chi-square. The analysis was restricted to species with >= 10 individuals, and only those species with chi-square > 6.63 (corresponding to p< 0.01) have been included in the table.

Kydia calycina Roxb.	L	16	93	7.67	22	26.77
	M	10	55	1.29	6	17.24
	H	204	1227	305.63	435	54.77
Terminalia crenulata Roth.	M	70	432	70.82	107	18.48
Helicteres isora L.	M	18	102	4.30	53	551.59
	H	247	1444	435.49	820	339.49
Agnogeissus latifolia (DC.)	L	24	147	18.19	43	33.86
	M	93	557	121.31	150	6.78
	H	72	414	36.40	66	24.08
Tectona Grandis L. f.	L	23	143	16.95	31	11.64
	H	37	225	10.17	27	27.08
Cassia fistula L.	L	15	81	6.26	15	12.19
	M	17	97	3.86	15	32.12
	H	37	222	10.03	36	67.25
Xeromphis spinosa (Thunb.)	H	46	287	16.12	35	22.11
Eriolanea quinquelocularis (Wt & Arn.)	H	11	66	0.89	4	10.94
Lagerstroemia parviflora Roxb.	M	17	99	3.94	17	43.27

the diameter. A regression of log-VCA vs log-diameter, however, brought about only a marginal improvement in the correlation coefficient. Interestingly, in contrast to the naive expectation, VCA seemed to vary sublinearly with the diameter; the slope of the regression line ranged between 0.2 and 0.3 for the three plots.

3. *Analysis of intra- and inter-specific affinities*

As mentioned earlier, one can examine if a species occurs significantly more often in its own neighbourhood than what its overall abundance would predict based on a random distribution. Table III shows the results of such an analysis for self-association. Nine species exhibit a high degree of self-association, with Helicteres isora showing a maximally clumped distribution. These results are consistent with the observed pattern of aggregation of these species in the whole 50 hectare plot[1], and thus provide support for the validity of the measure of self-association proposed in the present investigation.

A similar approach was used to analyse the cross-affinities of species, and the results are presented in Table IV. No significant associations are found in the L plot, perhaps due to the smaller sample sizes therein. The two other plots, however, show a number of pairs of species

Table IV

Analysis of association between species based on the chi-square test. The top portion corresponds to plot M, and the bottom portion to plot H. There were no statistically significant associations for plot L. For every species, the number of indivials of that species recorded in the plot is also indicated, followed by the chi-square values obtained for its association with all the other species. The symbol # indicates an empty cell (for self-association, not shown in this table), while 'n.s.' indicates that the chi-square value was not significantly higher than what was expected by chance (i.e, chi-square < 6.61, p>0.01). The dash ('-') indicates cells where the data was not large enough (expected frequency < 5.0) for a meaningful conclusion to be drawn from the test.

		1	2	3	4	5	6	
Kydia calycina	10	#	–	n.s.	–	–8.3	–7.3	–
Lagerstroemia microcarpa	23	–	#	n.s.	19.4	n.s.	n.s.	n.s.
Terminalia crenulata	70	n.s.	n.s.	#	n.s.	n.s.	n.s.	n.s.
Helictores isora	18	–	13.2	n.s.	#	–22.2	–13.6	–
Agnogeissus latifolia	93	–9.4	n.s.	n.s.	–23.5	#	n.s.	n.s.
Tectona grandis	57	–8.0	n.s.	n.s.	–14.4	n.s.	#	n.s.
Cassia fistula	17	–	n.s.	n.s.	–	n.s.	n.s.	#
		1	2	3	4	5	6	7
Kydia calycina	204	#	n.s.	n.s.	–31.0	n.s.	n.s.	n.s.
Lagerstroemia microcarp	13	n.s.	#	n.s.	n.s.	n.s.	–	–
Terminalia crenulata	88	n.s.	n.s.	#	–37.6	7.8	n.s.	n.s.
Helictores isora	248	–28.7	n.s.	–34.5	#	–59.5	–45.1	-6.9
Agnogeissus latifolia	72	n.s.	n.s.	9.5	–60.4	#	9.5	10.9
Tectona grandis	37	n.s.	–	n.s.	–46.0	8.8	#	n.s.
Cassia fistula	37	n.s.	–	n.s.	–10.1	9.3	n.s.	#

showing positive and negative affinities. A further advantage of the index defined here is that it is *not* symmetric for the two species involved – it is in principle possible to have such a distribution that species A, for example, may be significantly more often found in the neighbourhood of B, but not *vice versa*. The results shown in Table IV, however, show that the association is indeed symmetric, as it mostly should be based on biological interactions, thus providing further support for the validity of the index proposed in this study.

A negative association between two species may not be a true indicator of negative interactions between them – this could simply be a consequence of the two species having strong self-affinites. On the other hand, positive associations (*e.g.* as seen for Lagerstroemia microcarpa and Helicteres isora, Table IV) suggest that one could profitably explore the possible ecological interactions between that pair of species. Identification of assemblages of species, and the exploration of the patterns of their distribution are topics of considerable contemporary interest in community ecology[2,3]. The measure of the affinity between species, defined above can form an effective basis for obtaining species assemblages. Thus, in plot H, Anogeissus latifolia, Tectona grandis and Cassia fistula show not only high self-affinity, but a significant possitive association with each other as well (Table IV), hinting at the possibility of the presence of a distinct assemblage. Exploration of such patterns using more elaborate analysis and larger data sets are in progress.

4. *Area–perimeter relationships*

The areas of Delaunay triangles, and the VCAs obtained in the present investigation span a wide range of values. It would, therefore, be worthwhile to explore if their shapes show any systematic patterns *vis-á-vis* their sizes. This is normally done, following the prescription of Mandelbrot, by examining the area–perimeter relationships, using log–log plots and regression analysis; a value of slope away from 2 being suggestive of a fractal pattern. We have carried out the six regressions (Delaunay triangles and voronoi cells, for the three plots L, M, and H). Though the correlation coefficents were very high as usual (0.96), there were no substantial departures from a slope of 2. However, the three slopes for Delaunay triangles were somewhat lower than 2 (being 1.72, 1.84 and 1.84 with a standard error of 0.01); and for voronoi cells, somewhat higher than 2 (being 2.20, 2.17 and 2.10 with a standard error of 0.02) for the three plots L, M, and H, respectively.

A value lower than 2 implies that the area does not increase as fast with the perimeter as it would for a regular figure. This could happen if the larger Delaunay triangles are more likely to be long and narrow, compared to their smaller counterparts. This does seem to be borne out by a superficial examination of the figure of the Delaunay triangulation of the three plots (not shown). A similar argument suggests that larger voronoi cells are likely to be more 'circular' than the smaller ones, and thereby able to accomodate relatively more area for higher perimeters. In fact, larger voronoi cells do tend to have more neighbours (a positive correlation is seen in Table II), and are thus likely to have relatively more number of sides than the smaller ones. The ecological significance of these observations, if any, is, however, unclear at present.

Concluding remarks

Voronoi tessellations and related constructions have been used to a certain extent in ecology – most often for defining territories and home ranges of animals[10, 11]. They have also been used to examine the competetion between neighbouring plants for nutrients[12]. In this study, we have primarily focused on their use for constructing more objective indices of dispersion of plant species. These measures also promise to be of some utility for examining interspecific interactions.

We have also examined the association between voronoi cell areas and the diameter of the trees. The causal connection is not readily apparent. Bigger trees may have larger cells by their having prevented the germination or growth of other plants. On the other hand, a bigger cell could have prompted a faster growth by making more resources (or even more sunlight) to the trees. While at the moment it is not possible to distinguish between these two possibilities, it could be done in the future, when more data on the growth of these trees become available from our ongoing studies in the 50 hactare plot. It is also possible to examine the mortality rates, and the regeneration rates *vis-á-vis* areas of 'gaps' located around the dead trees in the plots. These investigations are under progress.

In summary, we have shown that the techniques borrowed from computational geometry, supplemented with widely available software which implements them on fast personal computer, can be of substantial use for the analysis of ecological data.

Acknowledgement

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