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Non-parametric tests and confidence regions for intrinsic diversity profiles of ecological populations

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SUMMARY

Evaluation of diversity profiles is useful for ecologists to quantify the diversity of biological communities. Measures of diversity profile can be expressed as a function of the unknown abundance vector. Thus, the estimators and related confidence regions and tests of hypotheses involve aspects of multivariate analysis. In this setting, using a suitable sampling design, inference is developed assuming an asymptotic specific distribution of the profile estimator. However, in a biological framework, ecologists work with small sample sizes, and the use of any probability distribution is hazardous. Assuming that a sample belongs to the family of replicated sampling design, we show that the diversity profile estimator can be expressed as a linear combination of the ranked abundance vector estimators. Hence we are able to develop a non-parametric approach based on a bootstrap in order to build balanced simultaneous confidence sets and tests of hypotheses for diversity profiles. Finally, the proposed procedure is applied on the avian populations of four parks in Milan, Italy. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: diversity profile; replicated sampling; bootstrap root estimate; balanced confidence regions

1. INTRODUCTION

When ecologists speak of the structure of a biological community they usually mean the number of individuals present, the number of species interacting and the proportion of each species. Diversity indexes incorporate some of these parameters into a single numerical value. Community diversity, diversity measurement and diversity comparisons have been important issues in ecological studies for more than four decades (for a review, see Grove, 1994).

Generally, measures of diversity can be expressed as function, say $g(\mathbf{N})$, of the unknown abundance vector $\mathbf{N} = [N_1, N_2, \ldots, N_s]$, where the ith element of $\mathbf{N}$ represents the number of units belonging to the ith species. Studies dealing with the topic of comparison communities by means of diversity indexes reached the overwhelming conclusion that no single diversity index adequately summarizes community structure. Hurlbert (1971) emphasized that different indexes may inconsistently rank a given pair of communities, in the sense that in making diversity comparisons, diversity may increase

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according to one index, but decrease according to a second index. Instead of a single index, one can use a parametric family of indexes whose members have varying sensitivities to the rare and abundant species. Several such families have been proposed (Hill, 1973; Patil and Taillie, 1976; Smith and Grassle, 1977). Perhaps a more useful way to compare diversity between communities is by the concept of intrinsic diversity ordering (Patil and Taillie, 1982). Community C_1 is intrinsically more diverse than C_2 if C_1 leads to C_2 by a finite sequence of

- introducing a species
- transferring abundance from more to less abundant species without reversing the rank-order of the species
- relabelling species.

Furthermore, following Patil and Taillie, a diversity profile approach can be developed by defining the right tail-sum of the ranked abundance vector:

$$T_j = \frac{1}{N}\sum_{i=j+1}^{s} N_{(i)}, \qquad j = 1, 2, \ldots, s-1 \tag{1}$$

where $N_{(1)} \geq \cdots \geq N_{(s)}$ are the ranked abundance, $N = \mathbf{1}^{\mathrm{T}}\mathbf{N}$ is the population total and $T_s = 0$ and $T_0 = 1$.

The convex curves obtained by plotting the (j, T_j) pairs are termed intrinsic diversity profiles and, any intrinsic diversity ordering, where present, can be determined by these diversity profiles. Let $\mathbf{T}_{C_1}$ and $\mathbf{T}_{C_2}$ be the intrinsic diversity profiles of community C_1 and C_2, respectively. The possible outcomes are:

- if $\mathbf{T}_{C_1} \leq \mathbf{T}_{C_2}$, then C_2 is more intrinsically diverse than C_1;
- if $\mathbf{T}_{C_2} \leq \mathbf{T}_{C_1}$, then C_1 is more intrinsically diverse than C_2;
- if $\mathbf{T}_{C_1} = \mathbf{T}_{C_2}$, then there is no difference in diversity between C_1 and C_2;
- if $\mathbf{T}_{C_1}$ crosses $\mathbf{T}_{C_2}$, then the two communities are not comparable with respect to diversity.

The main purpose of this article is to construct confidence sets for the intrinsic diversity profile of a community and to test hypotheses in order to compare communities according to their diversity. Fattorini and Marcheselli (1999) developed a procedure relying on the requirement of normality of the profile estimator. On the other hand, Marcheselli (2000) proves that the limiting distribution of this estimator may differ from multivariate normal distribution. More generally, the use of a given probability distribution is probably hazardous since the ecologist may be required to accept specific properties that may not be verified experimentally or otherwise. An alternative non-parametric methodology based on the bootstrap is pursued in this article. In Section 2 the methodology of constructing a bootstrap confidence region for the intrinsic diversity profile is presented. We extend this approach in Section 3 in order to test the presence of an intrinsic diversity ordering between two communities under study. Finally, in Section 4, the developed procedure is applied to a real data set. We conclude this section with some consideration about the opportunity of using a suitable sampling design to allow the use of bootstrap on biological populations and introduce some notation.

The intrinsic diversity profile is a function of the unknown ranked relative abundance vector $\mathbf{p} = (p_{(1)}, p_{(2)}, \ldots, p_{(s)})$, which in turn is a function of the ranked abundance vector as $p_{(i)} = N_{(i)}/N$ for $i = 1, 2, \ldots, s$. Accordingly, the problem lies in estimating $\mathbf{p}$ by means of a suitable sampling design and consequently estimating $\mathbf{T}(\mathbf{p})$. Even though the straightforward use of simple random sampling ensures fine results on abundance and diversity index estimation (Blyth, 1958; Bowman *et al.*, 1971; Adams and McCune, 1979), in real surveys it is not easy to take a random sample of individuals since biological populations are inevitably heterogeneous in time and space and rarely have a list frame. Pielou (1966) attempted to solve this sampling problem by using a cumulative pooled quadrat sampling design. Recently, Barabesi and Fattorini (1998) have adopted the replicated use of several line and point samplings for abundance and diversity estimation. Di Battista (2002) proposed adaptive sampling for estimating diversity index with rare, geographically clustered populations.

Without dealing here with these sampling techniques (for detailed reviews on sampling ecological communities, see De Vries (1986), Buckland *et al.* (1993) and Seber (1982)), let us start with a sample of distinct units selected from the population by using a given design. Then, owing to the standard Horwitz–Thompson theory, an unbiased estimator of $\mathbf{p}$, say $\hat{\mathbf{p}}$, is available. Accordingly, if the sampling procedure is independently replicated n times, the n samples provide n i.i.d. unbiased estimators for $\mathbf{p}$, say $\mathbf{n} = \hat{\mathbf{p}}_1, \ldots, \hat{\mathbf{p}}_n$ and an improved estimator for $\mathbf{p}$ is given by

$$\bar{\pi}_n = \frac{1}{n}\sum_{i=1}^{n}\hat{\mathbf{p}}_i \tag{2}$$

with variance–covariance $n^{-1}\mathbf{V}$.

Moreover, an unbiased and consistent estimator for $\mathbf{V}$ may be straightforwardly obtained by the variance–covariance matrix of the n estimates,

$$\mathbf{V}_n = \frac{1}{n-1}\sum_{i=1}^{n}(\hat{\mathbf{p}}_i - \bar{\mathbf{p}}_n)(\hat{\mathbf{p}}_i - \bar{\mathbf{p}}_n)^{\mathrm{T}} \tag{3}$$

In this setting the now-familiar non-parametric bootstrap method (Efron, 1982) may be suitably adopted on the i.i.d. samples $\hat{\mathbf{p}}_1, \ldots, \hat{\mathbf{p}}_n$.

Finally, we point out that if replicated sampling is not available then bootstrap procedures have to be modified to take into account the non-i.i.d. nature of the data as in real surveys the sample design without replacement is generally suggested. Recently, several bootstrapping methods for sampling without replacement have been proposed (Bickel and Freedman, 1984; Booth *et al.*, 1994).

2. CONFIDENCE SETS

Following the notation of Section 1, we express the intrinsic diversity profile in (1) as a linear function of the ranked relative abundance vector $\mathbf{p}$. Let $a_1, \ldots, a_{s-1}$ be the set of standard basis of $\mathcal{R}^{s-1}$ and define

$$\mathbf{b}_l = \sum_{j=1}^{s+1-l} a_j, \qquad l = 1, 2, \ldots, s-1$$

and $B = \{\mathbf{b}_l; l = 1, 2, \ldots, s-1\}$. Let C be a community with relative ranked abundance vector $\mathbf{p}$; then

$$\mathbf{T}(\mathbf{p}) = \{T_{\mathbf{b}}(\mathbf{p}) = \mathbf{b}'\mathbf{p} : \mathbf{b} \in \mathbf{B}\} \tag{4}$$

turns out to be the intrinsic diversity profile of community C. In this framework, the procedure of Beran (1988) may be implemented in order to obtain balanced simultaneous confidence sets for the intrinsic diversity profile $\mathbf{T}(\mathbf{p})$. This simultaneous confidence set is to have overall coverage probability $1-\alpha$ for $\mathbf{T}(\mathbf{p})$. Moreover, it is balanced in the sense that the coverage probability for the confidence statement concerning each right tail-sum $T_{\mathbf{b}}(\mathbf{p})$ remains unchanged as $\mathbf{b}$ varies. Finally, this method is non-parametric, whereas other methods such those of Tukey (1953), Scheffe' (1953) and Richmond (1982) become worthless if the components of $\mathbf{p}$ are heteroscedastic, dependent and not normally distributed.

Some new notations are needed before we proceed. Let $\mathbf{n}^* = (\hat{\mathbf{p}}_1^*, \ldots, \hat{\mathbf{p}}_n^*)$ be a bootstrap sample obtained by resampling with replacement from $\hat{\mathbf{p}}_i'$s. The bootstrap counterparts of $\bar{\mathbf{p}}_n$ and $\mathbf{V}_n$ are indicated by $\bar{\mathbf{p}}_n^*$ and $\mathbf{V}_n^*$, respectively. Define the studentized root for $T_{\mathbf{b}}(\mathbf{p})$, which is a functional depending on both the sample $\mathbf{n}$ and $T_{\mathbf{b}}(\mathbf{p})$, as

$$R_{n,\mathbf{b}}(\mathbf{n}, T_{\mathbf{b}}(\mathbf{p})) = n^{1/2} \frac{\mathbf{b}(\hat{\mathbf{p}}_n - \mathbf{p})}{[\mathbf{b}'\mathbf{V}_n\mathbf{b}]^{1/2}} \tag{5}$$

Let $L_{n,\mathbf{b}}$ and $U_{n,\mathbf{b}}$ denote consistent estimates for the $\beta/2$-th and the $(1-\beta/2)$-th quantiles of the distribution $H_{n,\mathbf{b}}(\mathbf{p})$ of the root $R_{n,\mathbf{b}}$ and let $H_{\sup}(\mathbf{p})$ and $H_{\inf}(\mathbf{p})$ be the cdf of the transformed root $\sup\{H_{n,\mathbf{b}}(R_{n,\mathbf{b}}, \mathbf{p}) : \mathbf{b} \in \mathbf{B}\}$ and $\inf\{H_{n,\mathbf{b}}(R_{n,\mathbf{b}}, \mathbf{p}) : \mathbf{b} \in \mathbf{B}\}$, respectively. A resulting confidence region for $T_{\mathbf{b}}(\mathbf{p})$ takes the form

$$C_{n,\mathbf{b}} = \{t_{\mathbf{b}} \in T_{\mathbf{b}} : L_{n,\mathbf{b}} \le R_{n,\mathbf{b}}(t_{\mathbf{b}}) \le U_{n,\mathbf{b}}\} \tag{6}$$

where $T_{\mathbf{b}}$ denotes the set of all possible values of $T_{\mathbf{b}}(\mathbf{p})$. Simultaneously asserting the confidence sets $\{C_{n,\mathbf{b}}\}$ generates the following confidence set for $\mathbf{T}(\mathbf{p})$:

$$C_n = \{t \in \mathbf{T} : L_{n,\mathbf{b}} \le R_{n,\mathbf{b}}(t_{\mathbf{b}}) \le U_{n,\mathbf{b}}, \forall\, \mathbf{b} \in \mathbf{B}\} \tag{7}$$

where $\mathbf{T}$ denotes the set of all possible values of $\mathbf{T}(\mathbf{p})$.

The availability of bootstrap estimates for the unknown roots distributions enlarges the possibilities for simultaneous inference. The proposed bootstrap version of simultaneous confidence set C_n is obtained by taking the critical values in (7) to be

$$L_{n,\mathbf{b}} = H_{n,\mathbf{b}}^{*-1}\left[H_{\inf}^{*-1}\left(\frac{\alpha}{2}\right)\right] \tag{8}$$

and

$$U_{n,\mathbf{b}} = H_{n,\mathbf{b}}^{*-1}\left[H_{\sup}^{*-1}\left(1-\frac{\alpha}{2}\right)\right] \tag{9}$$

where $H_{n,\mathbf{b}}^*$, $H_{\inf}^*$ and $H_{\sup}^*$ are the bootstrap distribution estimates of $H_{n,\mathbf{b}}$, $H_{\inf}$ and $H_{\sup}$, respectively. The asymptotic coverage probability of confidence set C_n and its component confidence sets $\{C_{n,\mathbf{b}}\}$ are given in theorem 4.1 of Beran (1988). We point out that theorem assumptions are satisfied here, being our framework equivalent to example 1 in Beran (1988).

Finally, we emphasize that the bootstrap estimates $\mathbf{V}^*$ of the covariance matrix $\mathbf{V}$ cannot be used since the resulting diversity profile fails to be convex.

3. HYPOTHESIS TESTING

In order to evaluate and monitor biodiversity at different spatial (or temporal) scales, suitable hypotheses for comparing diversity have to be assessed. The testing question is if diversity is the same for each community (equivalence) or there is a habitat (temporal) diversity effect (dominance) or, finally, the communities are not intrinsically comparable. Gove *et al.* (1994) proposed a jackknifing approach along with diversity indexes which are isotonic with respect to the intrinsic diversity ordering but '*this procedure must be viewed as only an approximate test because it involves difficult and unresolved questions of simultaneous inference*'. Alternatively, under asymptotic multinormality of the sample intrinsic diversity profile, Fattorini and Marcheselli (1999) proposed an asymptotically conservative procedure to compare couples of diversity profiles on the basis of a method previously proposed by Bishop *et al.* (1991) for making inference on Lorenz curves. Now, we extend the procedure of the previous section so that non-parametric inference can be made about intrinsic diversity orderings. Using a bootstrap we implement a procedure that even though the assumed model fails, still stays optimal under some minor regularity conditions. Denote the diversity profiles of communities C_1 and C_2 by $\mathbf{T}_1$ and $\mathbf{T}_2$, respectively. Then the null hypothesis is

$$\mathrm{H}_0 : \mathbf{T}_1 = \mathbf{T}_2$$

against the alternative $\mathrm{H}_1 : \mathbf{T}_1 \neq \mathbf{T}_2$. Let $\boldsymbol{\theta} = \mathbf{T}_1 - \mathbf{T}_2$ be the $(s-1)$-vector of the difference in the right tail-sums of the two communities. Thus, the equivalence hypothesis of the two profiles may be written as

$$\mathrm{H}_0 : \boldsymbol{\theta} = \boldsymbol{\theta}_0 = 0$$

so that a suitable $(s-1)$-components statistic to evaluate departures from the null hypothesis is

$$G_{n,\mathbf{b}}(\boldsymbol{\theta}_0) = \frac{\bar{\boldsymbol{\theta}} - \boldsymbol{\theta}_0}{\left[\dfrac{\mathbf{b}'\mathbf{V}_1\mathbf{b}}{n_1}\right]^{\frac{1}{2}} + \left[\dfrac{\mathbf{b}'\mathbf{V}_2\mathbf{b}}{n_2}\right]^{\frac{1}{2}}} \tag{10}$$

for every value of $\mathbf{b} \in \mathbf{B}$, where $\bar{\boldsymbol{\theta}} = \{\mathbf{b}'(\bar{\mathbf{p}}_1 - \bar{\mathbf{p}}_2) : \mathbf{b} \in \mathbf{B}\}$ is an estimate of $\boldsymbol{\theta}$, and $\bar{\mathbf{p}}_1$ and $\bar{\mathbf{p}}_2$ are the sample estimates of $\mathbf{p}_1$ and $\mathbf{p}_2$ with covariance matrices $\mathbf{V}_1$ and $\mathbf{V}_2$, respectively.

The key idea here is to test hypothesis $\mathrm{H}_0 : \mathbf{T}_1 = \mathbf{T}_2$ by constructing a confidence set for parameter $\boldsymbol{\theta}$ in order to examine how plausible it is for $\boldsymbol{\theta}$ to assume the values $\boldsymbol{\theta}_0 = 0$ if $\boldsymbol{\theta}$ actually followed the bootstrap distribution. By applying the method of Section 3 to the roots $G_{n,\mathbf{b}}$ we generate a simultaneous confidence set for $\boldsymbol{\theta}$ that, under H_0, is asymtotically balanced and has a correct overall coverage probability. More explicitly, let $Q_{\mathbf{b}}(\boldsymbol{\theta}), Q_{\sup}(\boldsymbol{\theta})$ and $Q_{\inf}(\boldsymbol{\theta})$ be the cdf of $G_{\mathbf{b}}, \sup\{Q_{\mathbf{b}}(\boldsymbol{\theta}), \mathbf{b} \in \mathbf{B}\}$ and $\inf\{Q_{\mathbf{b}}(\boldsymbol{\theta}), \mathbf{b} \in \mathbf{B}\}$, respectively. Let $Q^*_{\mathbf{b}}(\boldsymbol{\theta}), Q^*_{\sup}(\boldsymbol{\theta})$ and $Q^*_{\inf}(\boldsymbol{\theta})$ denote the corresponding bootstrap estimates of these cdfs' obtained by taking bootstrap data from the empirical distributions of the two communities separately. The smoothness assumption on $\mathbf{T}(\mathbf{p})$ yields consistency of the bootstrap procedure (see Di Ciccio and Romano (1988), example 3.3).

We define a $1-\alpha$ simultaneous confidence set for $\boldsymbol{\theta}$ as

$$D_{\boldsymbol{\theta},1-\alpha} = \{\boldsymbol{\theta} : l_{\mathbf{b}} \le G_{\mathbf{b}} \le u_{\mathbf{b}}, \mathbf{b} \in B\} \tag{11}$$

where the critical values are obtained by

$$l_{\mathbf{b}} = Q_{\mathbf{b}}^{*-1}\left[Q_{\inf}^{*-1}\left(\frac{\alpha}{2}\right)\right] \tag{12}$$

and

$$u_{\mathbf{b}} = Q_{\mathbf{b}}^{*-1}\left[Q_{\sup}^{*-1}\left(\frac{\alpha}{2}\right)\right] \tag{13}$$

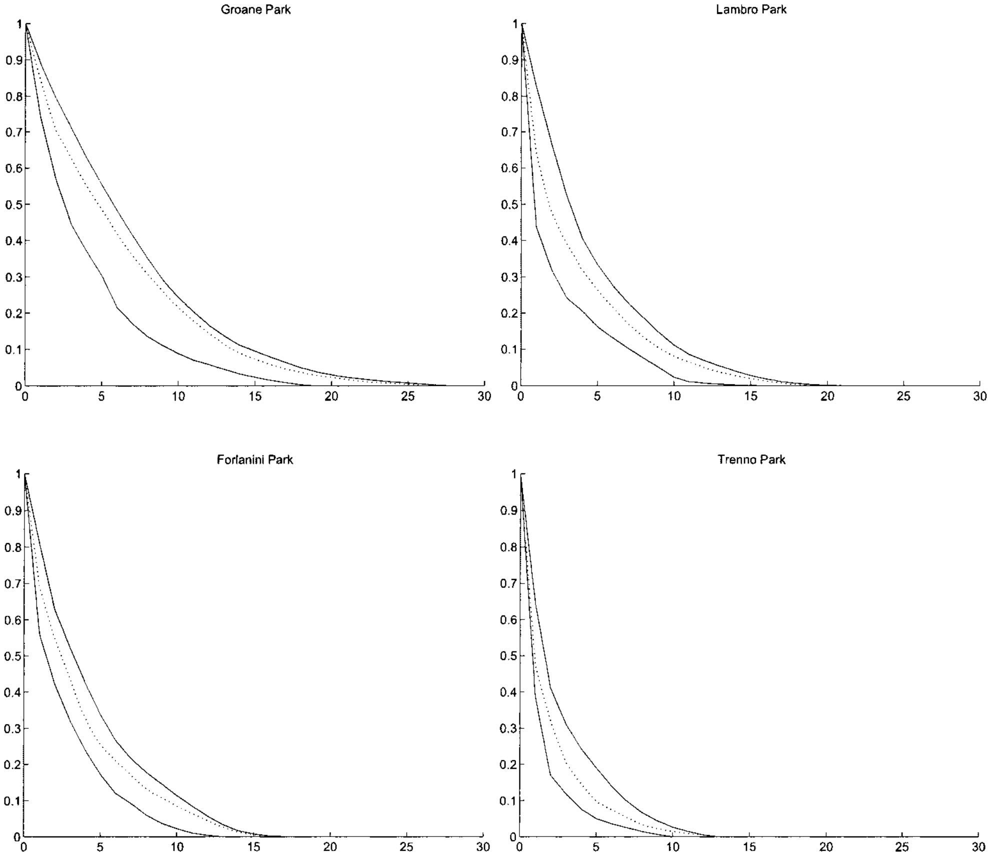

Figure 1. Diversity profile estimates (dotted line) and 0.95 simultaneous confidence bands (solid line)

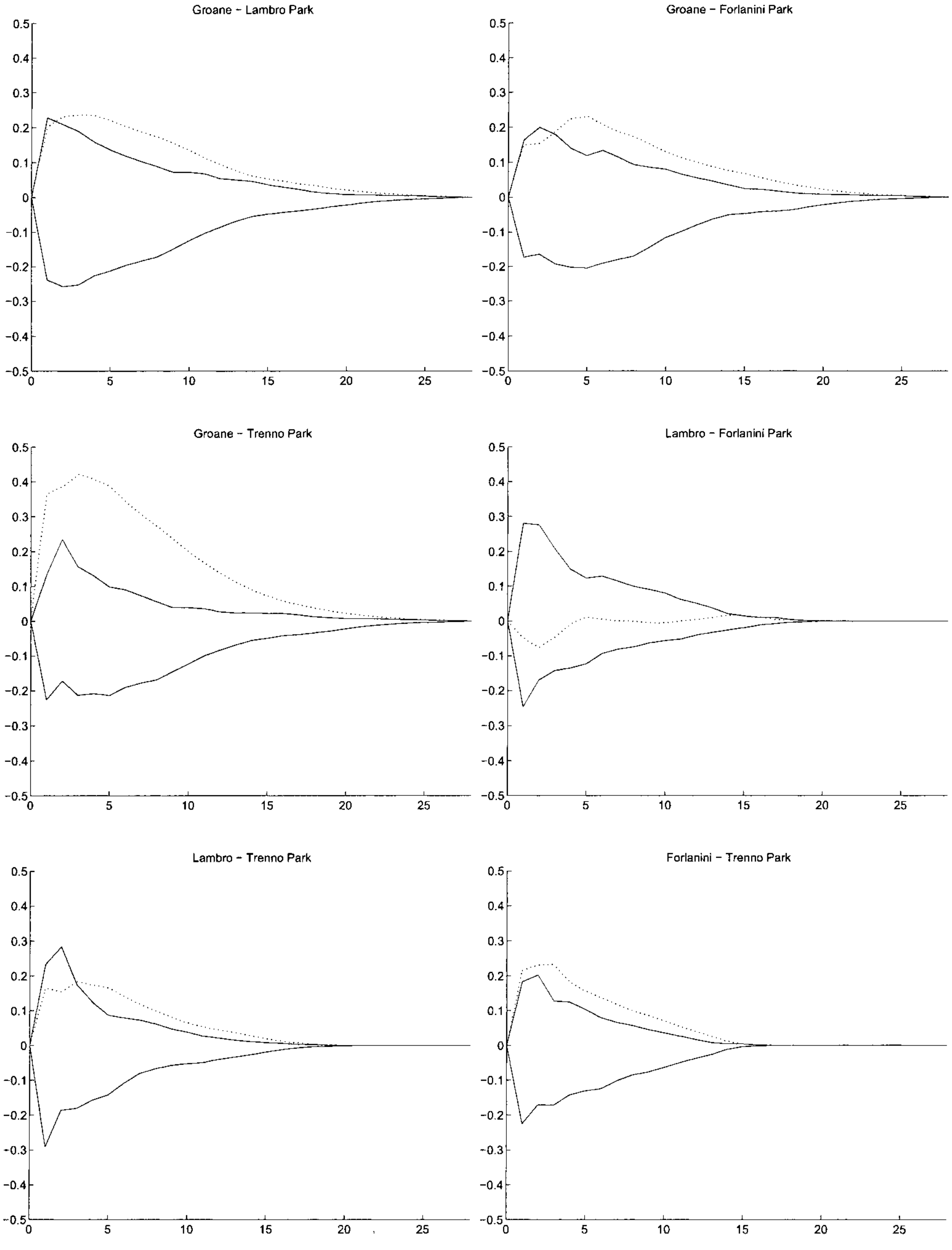

Figure 2. Profile diversity difference estimates (dotted line) and 0.95 simultaneous confidence sets (solid line)

On the basis of (11) we can derive a decision rule as follows:

- accept $H_0 : \mathbf{T}_1 = \mathbf{T}_2$ if $\bar{\boldsymbol{\theta}}$ belongs to the region $D_{\boldsymbol{\theta},1-\alpha}$
- reject H_0 and accept dominance if $\bar{\boldsymbol{\theta}} \geq D_{\boldsymbol{\theta},1-\alpha}$ or, alternatively, if $\bar{\boldsymbol{\theta}} \leq D_{\boldsymbol{\theta},1-\alpha}$
- finally, if both $\bar{\boldsymbol{\theta}} \geq D_{\boldsymbol{\theta},1-\alpha}$ and $\bar{\boldsymbol{\theta}} \leq D_{\boldsymbol{\theta},1-\alpha}$ hold, then reject H_0; the implication is that the profiles intersect and the communities C_1 and C_2 are not intrinsically comparable.

4. AN APPLICATION

The proposed procedures were carried out on the avian communities of four parks in Milan (Italy): Groane, Lambro, Forlanini and Trenno parks. A detailed description of the sampling design is given in Fattorini and Marcheselli (1999). We remark that independent estimates $\hat{\mathbf{p}}_i \, (i = 1, 2, \ldots, n)$ were available from the replicated use of a suitable encounter design. Accordingly the procedures described in Sections 2 and 3 can be applied. For each park we compute the diversity profile as $\mathbf{T}(\bar{\mathbf{p}}_n)$ and derive simultaneous confidence sets using the previously described non-parametric model for the data. In Figure 1, the resulting diversity profiles (dotted line) and the corresponding 0.95 bootstrap confidence regions (solid line) for the four parks are shown. Furthermore, in order to rank the parks according to their diversity we evaluate an estimate of $\boldsymbol{\theta}$, the difference in the diversity profile for each of the possible couples of parks. Under the null hypothesis of no difference in diversity we derive a 0.95 simultaneous confidence set for $\boldsymbol{\theta}$. Plots of the observed values of $\bar{\boldsymbol{\theta}}$ (dotted line) and the corresponding 0.95 bootstrap confidence regions (solid line) are displayed in Figure 2. Therefore, if the values of $\bar{\boldsymbol{\theta}}$ are always inside the confidence region then we accept the null hypothesis and we conclude that the two parks are intrinsically equivalent. The converse is when values of $\bar{\boldsymbol{\theta}}$ fall outside the confidence region. In this case we conclude that the parks are intrinsically diverse. From the analysis of Figure 2, Groane park and Trenno park turn out to be the most intrinsically diverse and the least intrinsically diverse, respectively. Moreover, Lambro and Forlanini parks can be located at an intermediate diversity level, being equivalent parks in terms of intrinsic diversity profiles.

Finally, it is worthwhile to remark that these results are obtained without any model assumption either for the species abundance or for the profile estimator. The procedure attempts to reflect the true shape of the underlying distribution.

In particular, the resulting confidence regions in Figure 1 clearly show departure from symmetry for Groane park. This could be considered vital to the investigator especially in a biological framework where distributions might be heavily skewed and asymmetric.

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