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# Estimation of local extinction rates when species detectability covaries with extinction probability: is it a problem?

**Stephanie Jenouvrier and Thierry Boulinier**

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Estimating the rate of change of the composition of communities is of direct interest to address many fundamental and applied questions in ecology. One methodological problem is that it is hard to detect all the species present in a community. Nichols et al. presented an estimator of the local extinction rate that takes into account species probability of detection, but little information is available on its performance. However, they predicted that if a covariance between species detection probability and local extinction rate exists in a community, the estimator of local extinction rate complement would be positively biased.

Here, we show, using simulations over a wide range of parameters that the estimator performs reasonably well. The bias induced by biological factors appears relatively weak. The most important factor enhancing the performance (bias and precision) of the local extinction rate complement estimator is sampling effort. Interestingly, a potentially important biological bias, such as the covariance effect, improves the estimation for small sampling efforts, without inducing a supplementary overestimation when these sampling efforts are high. In the field, all species are rarely detectable so we recommend the use of such estimators that take into account heterogeneity in species detection probability when estimating vital rates responsible for community changes.

*S. Jenouvrier, Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, FR-79360 Villiers en Bois, France (jenouvrier@cebc.cnrs.fr). – T. Boulinier, Centre d'Ecologie Fonctionnelle et Evolutive, CNRS – UMR 5175, Montpellier, France.*

Estimating the rate of change of the composition of communities is of direct interest to address many fundamental questions in ecology (Rosenzweig and Clark 1994, Doherty et al. 2003a), but also in relation to more applied questions linked with the conservation of biodiversity (Heywood 1995, Yoccoz et al. 2001). One methodological problem is that it is hard to detect all the species present in a community at a given location and time period, and thus it is necessary to account for that when one wants to infer rates of change in communities (Nichols et al. 1998a, Gu and Swihart 2004). This is especially the case if such estimates are used to compare the dynamics of communities in contrasting situations (e.g. habitats), as the probability of detecting species may be differ according to the particular situations. Higher apparent local extinction rates could be due to a confounding effect of the relative species detection probabilities, which could be linked to their local abundance (Doherty et al. 2003b, Alpizar-Jara et al. 2004). For instance, in the case of animal communities in landscapes that are more or less fragmented, results may be biased if animal species are more or less likely to be detected in landscapes with different levels of fragmentation.

Estimators of species richness that take into account species probability of detection have been available to ecologists for a long time (Burnham and Overton 1979, reviewed by Bunge and Fitzpatrick 1993, Colwell and

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Coddington 1994, Nichols and Conroy 1996, Boulinier et al. 1998, Gotelli and Colwell 2001). Recently, interest has intensified in the development and evaluation of estimators to measure turnover of species assemblages, and Chao et al. (2005) proposed for instance a method to estimate similarity between communities taking into account unseen shared species. Nichols et al. (1998a) proposed estimators for parameters of the rates of change of communities, and in particular local extinction and turnover rates. Their approach is based on an analogy with work at the population level (Williams et al. 2002), and relies on the robust design of Pollock (1982), which enables estimation of parameters of populations when there are heterogeneous probabilities of detection of individuals. With this approach, the estimate of the local extinction rate complement (LERC, or ($\phi_{ij}$) in a demographic context) between two primary sampling period i and j is: $\hat{\phi}_{ij} = \hat{M}_j^{Ri}/R_i$, where $R_i$ is the number of species observed at the primary sampling period i, and $\hat{M}_j^{Ri}$ is the estimated number of these species still present at the primary sampling period j (Nichols et al. 1998a). Secondary sampling periods within the second primary sampling period enable the use of a "closed community" estimator (by analogy to a "closed population", Williams et al. 2002) to estimate the number of species detected the previous period ($\hat{M}_j^{Ri}$). This estimator can be chosen from among a series of estimators that rely on different hypotheses regarding the way species detection probability may vary, e.g. among species or time period/occasion (Otis et al. 1978). Practically, the use of the jackknife estimator of species richness developed to account for heterogeneity in the probability of detecting species (Burnham and Overton 1978, 1979, Boulinier et al. 1998, Nichols et al. 1998a, 1998b) to compute the estimators of rates of change has been suggested and can be implemented using an internet based program (Hines et al. 1999, COMDYN).

One potential problem with the estimator of the local extinction rate is that it is based on a ratio involving a sub-sample of the community that may have specific characteristics, one important characteristic being that they have been detected at the first primary sampling period. Nichols et al. (1998a) did not present any study of the performance of their estimator but stressed that, as the estimator of the local extinction rate was conditioned on the species that had been detected at the first primary sampling session, it could be biased towards lower values if species that are the most detected are also the most abundant, and thus possibly the most likely not to go extinct due to environmental and/or demographic stochasticity. Indeed, the local extinction rate should depend on the number of individuals as a result of demographic or environmental stochasticity (Gilpin and Soulé 1986, Kinney 1997). Nichols et al. (1998a) thus predicted that if such a covariance between detection probability and local extinction rate exists in a community, the species more likely to be detected during the primary sampling session may be the highly detectable ones, so that the LERC would thus be positively biased. Indeed, if species are more detectable because they are more abundant, they will obviously have more chance of being present and identified during the second primary session than species not yet detected. This can lead to an overestimation of both the numbers of shared species between two sampling sessions (i and j) and the LERC ($\phi_{ij}$).

Alpizar-Jara et al. (2004) provided strong empirical evidence that local extinction probability covaries negatively with species detection probability and probably abundance of individuals within species. They also suggested an ad hoc weighted estimator to try to reduce bias in the extinction probability estimator. The difference between the original estimator and the new weighted estimator was much smaller than they expected, suggesting that the bias associated with the original estimators is not large. However, their empirical and simulation work was based on the North American Breeding Bird Survey, and they highlighted that analyses of different kinds of community-level data will likely merit additional simulations tailored to other sampling situations.

Here, we investigate, using simulations over a wide range of parameters, the bias induced by the relationship between detection probability and local extinction probability. The bias appears to be relatively small, and we show that the most important factor affecting the performance (bias and precision) of the local extinction rate complement estimator is the sampling effort. Interestingly, the estimator of the LERC performs actually slightly better when there is a positive covariance between the probability of species to be detected and their probability to "survive". Such estimators of extinction and turnover rates based on capture–recapture modelling are thus of much practical value for analysing data to study the dynamics of biodiversity when species detection probabilities cannot be assumed to equal one.

## Simulation approach

In order to study the performance of the estimator, we simulated (1) a virtual community undergoing temporal change in composition and (2) a sampling of that community under a robust design (Williams et al. 2002). We simulated a community of N species, in which species could go extinct between two primary sampling sessions (PSS). Within each PSS, the community is considered closed and we could set the number of secondary sampling occasions. The overall probability of detection over a PSS will depend on both the average species detection probability at each occasion, p, and the number of secondary sampling occasions (Nichols et al. 1998a). With the sets of parameters we used for each combination of number of occasions and probability of detection at each occasion, the probability of detection at the scale of a PSS varied between 20% and 100% (e.g. 5 occasions and $p = 0.05$ leads to a $p_{PSS} =$ 22.6%; 20 occasions and $p = 0.30$ leads to $p_{PSS} = 99.9\%$). For each group of species, we could set a local extinction rate ($LER = 1 - \phi$).

By analogy with Carothers (1973), we considered two distinct groups of species in order to investigate the potential effect of heterogeneity among species on the performance of the estimator: one group stood for highly detectable species and the other for less detectable ones. With a mean species detection probability p and a coefficient of variation of species detection probability CV, the respective detectabilities of the two groups at each secondary sampling occasion were set to: $p_H = p(1+CV)$ and $p_L = p(1-CV)$. The higher the CV, the greater the difference in detection probability is between the two groups. Differences in the probability of detection among species may be due to factors such as variation in abundance and/or morphological and behavioural characteristics. Detectability will also be affected by sampling methods and effort. We simulated the pattern of detection/non-detection of each species over each series of occasions using a Bernoulli drawing of probability $p_H$ or $p_L$. We used this simulated community sampling to estimate the LERC ($\hat{\phi}_{ij}$). Summary statistics needed were the number of species detected exactly i times ($f_i$) over the series of secondary sampling occasions and the number of species detected on each secondary sampling occasion i ($n_i$). Computations were implemented using COMDYN4 (Hines et al. 1999), which is available online on the internet (http://www.mbr-pwrc.usgs.gov/software/comdyn.html). We then calculated the bias and precision after performing a hundred simulations, in order to assess the performance of the LERC estimator. This bias is estimated as the difference between the mean of the estimators over the hundred simulations $\bar{\hat{\phi}}_{ij}$ and the fixed value of the LERC $\phi_{ij}$. The percent relative bias was calculated as: % bias$(\hat{\phi}_{ij}) = 100$ $(\bar{\hat{\phi}}_{ij} - \phi_{ij})/\phi_{ij}$. The standard deviation computed from the hundred simulations represents the precision of the estimator. To account for both the estimator bias and precision, we used the root mean square error (rmse): rmse $(\hat{\phi}_{ij}) = \sqrt{\text{biais}(\hat{\phi}_{ij})^2 + \text{var}(\hat{\phi}_{ij})}$.

We considered different factors that could affect the performance of the LERC estimation: (1) the methodology used, i.e. the capture–recapture estimation approach vs the use of simple counts of species, (2) measures of sampling effort, i.e. the number of secondary occasions and the probability of detection at each secondary occasion, (3) intrinsic features of the community, i.e. the number of species, the heterogeneity in their detection probability, and the covariance effect between species detection probability and extinction probability. To study the covariance effect between species detection probabilities and extinction probabilities, we set a low local extinction rate for the highly detectable group of species and a high local extinction rate for the less detectable group of species. For this study, we choose a total number of species $N = 50$ and $CV = 0.5$.

To compare the importance of these different factors we used a variance–covariance analysis (ANCOVA, PROC GLM, SAS Inst.). We could not use the bias, precision or rmse as a measure of the performance of an estimator in our ANCOVA analysis because they are function of the number of simulations. Therefore, the effects of different factors on the performance of the LERC estimator was assessed considering $I_k = |(\hat{\phi}_k - \phi)/\phi|$ for each simulation run $k \in [1, 20]$ as the dependent variable. We compared the value of the F-statistics because the degrees of freedom of the different factors are equal, whereas we could not use the significance value of the ANCOVA because it is function of the number of simulations (here 20 for all treatment). To respect the hypothesis of the ANCOVA, we used the transformation $\arcsin(I_i^{1/2})$.

## Results

The estimations of LERC, $\hat{\phi}$, depended essentially on the choice of the methodology (CMR or count of species) and the sampling effort (Table 1). The LERC estimated with the CMR method is much less biased than based on the simple counts of species (Table 2). For example, Table 2 showed that for 20 secondary sampling occasions and a detection probability at each occasion of 0.05, the bias of $\hat{\phi}$ using the CMR method is $-8\%$ and for the counts of species $-33\%$. In addition, the rmse of the LERC estimator with the CMR method was lower than the rmse of the LERC based on the simple counts of species, indicating that the LERC of the jackknife estimator performed better.

With both approaches, the sampling effort, and especially the number of sampling occasions, is the most important effect that affects the bias of the estimation of the LERC $\hat{\phi}$, (Table 1). Estimates of LERC are highly negatively biased when the number of secondary sampling occasions and the detection probability at each occasion are low (detection probability at the scale of PSS $<50\%$, Table 2). When the number of secondary sampling occasions and the detection probability increase, estimates of LERC $\hat{\phi}$ tend towards the true fixed LERC with a slight overestimation for the LERC jackknife estimator when the sampling effort is very high (detection probability at the scale of PSS near

Table 1. Comparison of the importance of the different factors affecting the performance of the estimator of local extinction rate complement (LERC): (1) methodological factors: capture–recapture approach vs simple ratio of species counts (methodology), sampling effort (number of occasions and detection probability at each occasion), (2) intrinsic features of the community (number of species, heterogeneity between species detection probabilities and covariance effect between species detection probabilities and extinction probabilities). The effects of these factors on the performance of the estimator $\hat{\phi}$ is assessed using $I_k = |(\hat{\phi}_k - \phi)/\phi|$ (see methods). We use the transformation $X_{Ti} = \arcsin\{\sqrt{X}\}$ to normalize the residual for the ANCOVA analysis.

| Source | DF | F |
|---|---|---|
| Model | 16 | 246.49 |
| Error | 3223 | |
| Totals corrected | 3239 | |
| Number of occasions | 1 | 235.47 |
| Methodology | 1 | 231.34 |
| Methodology × number of occasions | 1 | 153.26 |
| Methodology × number of species | 1 | 116.39 |
| Methodology × detection probability | 1 | 94.48 |
| Detection probability | 1 | 73.02 |
| Number of occasion × number of species | 1 | 53.06 |
| Number of occasion × heterogeneity between species detection probability | 1 | 51 |
| Heterogeneity between species | 1 | 30.57 |
| Detection probability × number of species | 1 | 28.67 |
| Number of species | 1 | 26.15 |
| Covariance effect | 1 | 19.6 |

100%) (Fig. 1, Table 2). In addition, as expected, the precision of the estimator of the LERC increases with the number of secondary sampling occasions and the probability of detection. For example, for a detection probability at each secondary occasion of 0.15, the std ($\hat{\phi}_{\text{jackknife}}$) decreases between 0.20 and 0.08 when the number of secondary occasions increases between 2 and 20. More generally, the rmse of the LERC estimator decreases when sampling effort increases (Table 2). Therefore, the estimator performed better (i.e. is less biased and more precise) when the sampling effort was increased.

The intrinsic biological effects due to community characteristics (number of species, the importance of having some heterogeneity between species and the covariance effect between species detection probabilities and extinction probabilities) are weak but visible in their interaction with the effects of the methodology and sampling effort (Table 1: interactions). In fact, they are most visible when the sampling effort is intermediate. When the sampling effort is low, the performance of the estimator of the LERC $\hat{\phi}$ is worse for the whole range of intrinsic community effects. However, when effort is high, the performance is good. For an intermediate sampling effort, when the number of species increases or/and the heterogeneity between species decreases and/or there is a covariance effect, the performance of the estimator of the LERC $\hat{\phi}$ is enhanced.

As predicted by Nichols et al. (1998a), we find that estimates of LERC were slightly positively biased when

Table 2. Simulation results for the local extinction rate complement estimator (LERC). The true parameter value were set to $\phi = 0.85$, with $\phi_H = 0.95$ and $\phi_L = 0.75$ in the cases for which a covariance effect was taken into account. The overall probability of detection over a primary sampling session (PSS) will depend on both the average species detection probability at each secondary sampling session (SSS), p, and the number of secondary sampling occasions (No.). With a mean species detection probability p and a coefficient of variation of species detection probability CV = 0.5, the respective probabilities of detection of the groups of highly detectable species and less detectable ones were $p_H$ and $p_L$. The number of species in the community was set to 50. % bias and rmse stand respectively for relative bias and root mean square error (Methods).

| No. | SSS level | | | | PSS level | | $\hat{\phi}$ based on count | | | $\hat{\phi}$ based on jackknife without covariance | | | $\hat{\phi}$ based on jackknife with covariance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | p | $p_H$ | $p_L$ | $p_{PSS}$ | $p_{PSS\,H}$ | $p_{PSS\,L}$ | $\hat{\phi}$ | %bias | rmse | $\hat{\phi}$ | %bias | rmse | $\hat{\phi}$ | %bias | rmse |
| 5 | 0.05 | 0.08 | 0.03 | 0.23 | 0.32 | 0.12 | 0.24 | −72.22 | 0.67 | 0.49 | −42.72 | 0.45 | 0.51 | −40.53 | 0.43 |
| 10 | 0.05 | 0.08 | 0.03 | 0.40 | 0.54 | 0.22 | 0.39 | −54.44 | 0.5 | 0.58 | −31.51 | 0.36 | 0.64 | −25.01 | 0.33 |
| 15 | 0.05 | 0.08 | 0.03 | 0.54 | 0.69 | 0.32 | 0.48 | −43.33 | 0.4 | 0.76 | −10.98 | 0.22 | 0.76 | −10.67 | 0.24 |
| 20 | 0.05 | 0.08 | 0.03 | 0.64 | 0.79 | 0.40 | 0.57 | −33.33 | 0.31 | 0.79 | −7.65 | 0.18 | 0.81 | −4.68 | 0.15 |
| 2 | 0.15 | 0.23 | 0.08 | 0.28 | 0.40 | 0.14 | 0.30 | −64.44 | 0.6 | 0.42 | −50.86 | 0.47 | 0.40 | −52.98 | 0.49 |
| 5 | 0.15 | 0.23 | 0.08 | 0.56 | 0.72 | 0.32 | 0.51 | −40.00 | 0.37 | 0.76 | −10.82 | 0.20 | 0.83 | −2.62 | 0.16 |
| 10 | 0.15 | 0.23 | 0.08 | 0.80 | 0.92 | 0.54 | 0.66 | −22.22 | 0.21 | 0.79 | −7.10 | 0.12 | 0.85 | 0.15 | 0.11 |
| 15 | 0.15 | 0.23 | 0.08 | 0.91 | 0.98 | 0.69 | 0.74 | −13.33 | 0.14 | 0.84 | −0.82 | 0.11 | 0.86 | 0.66 | 0.09 |
| 20 | 0.15 | 0.23 | 0.08 | 0.96 | 0.99 | 0.79 | 0.77 | −10.00 | 0.1 | 0.85 | −0.16 | 0.08 | 0.87 | 2.26 | 0.08 |
| 2 | 0.30 | 0.45 | 0.15 | 0.51 | 0.70 | 0.28 | 0.50 | −41.11 | 0.38 | 0.62 | −26.97 | 0.27 | 0.68 | −20.56 | 0.22 |
| 5 | 0.30 | 0.45 | 0.15 | 0.83 | 0.95 | 0.56 | 0.69 | −18.89 | 0.18 | 0.81 | −4.56 | 0.12 | 0.85 | 0.21 | 0.10 |
| 10 | 0.30 | 0.45 | 0.15 | 0.97 | 1.00 | 0.80 | 0.77 | −8.89 | 0.1 | 0.84 | −1.23 | 0.08 | 0.86 | 1.32 | 0.08 |
| 15 | 0.30 | 0.45 | 0.15 | 1.00 | 1.00 | 0.91 | 0.81 | −4.44 | 0.06 | 0.88 | 4.07 | 0.07 | 0.88 | 2.95 | 0.07 |

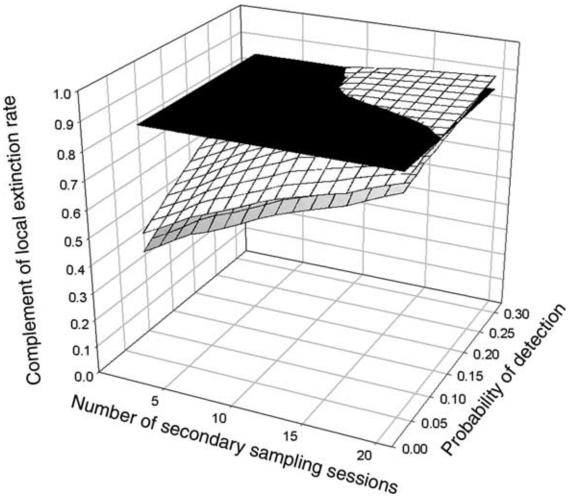

Fig. 1. Estimates of the local extinction rate complement (LERC) as a function of the effect of the covariance between species detection probabilities and extinction probabilities for different sampling situations. The black surface represents the fixed true value for the complement of local extinction rate, the white surface represents the value estimated when there is a positive covariance between detection and extinction probabilities, and the grey surface when there is no covariance between these variables (species richness = 50, coefficient of variation = 0.5, $\phi_{nocov} = 0.85$, $\phi_{covHigh} = 0.95$, $\phi_{covLow} = 0.75$).

there is a positive covariance between detection probability and LERC, regardless of the intensity of the sampling effort (Fig. 1, Table 2). We can note that when sampling efforts increased, the difference between both scenarios was reduced. As the covariance did not influence the LERC precision (e.g. for a detection probability at each occasion of 0.15 and 5 occasions, the std ($\hat{\phi}$) is 0.22 without covariance effect and 0.21 with a covariance effect), local extinction rate estimates were improved for low and intermediate sampling effort values when local extinction rate covaried with detection probability (Fig. 1).

## Discussion

Nichols et al. (1998a) stressed that if the probability of detection and the local extinction rate are both a function of species abundance, then the estimator of local extinction rate will be negatively biased. Alpizar-Jara et al. (2004) noted that there could be a spatial bias if the number of individuals in a species is related to the detection of this species at a specific location. They also showed that covariance between local extinction rate and detection probability may exist in studies of bird communities as with the North American Breeding Bird Survey. We can suppose that communities of similar species tend to be more affected by the effect of covariance. In fact, species detectability is likely a function of morphological and behavioural characteristics and because species that are taxonomically close will have a similar morphology and behaviour, variation in detection probability in such groups will largely be a function of abundance.

Here we have shown that covariance between detection probability and local extinction rate induces a positive bias in the LERC $\phi_{ij}$. However, as found by Alpizar-Jara et al. (2004), the effect of covariance in our study remains small. We showed that the effect of the covariance tended to be less important when sampling efforts were intense and that the sampling effort effect is a very important factor affecting the performance of the LERC. When the sampling effort is low, however, the estimator performs badly and estimates are largely underestimated. But the effect of covariance leads us to overestimate the LERC in comparison to situations in which values do not covary. So the biologically induced bias due to covariance compensates for the bias resulting from a low sampling effort. Therefore, even when the biological effect of covariance is present in a studied community, and despite a sampling effort of low intensity, estimations of LERC are improved. Conversely, if the effort of sampling is of high intensity, the difference between situations with and without covariance remains very small. As a result, in order to obtain a good estimator, it is crucial to increase the sampling effort even when local extinction rate and detection probability covary, especially as this effect cannot be controlled for during sampling.

Studying estimator performance is useful because it allows the determination of the relative importance of the different factors affecting the estimator. The results of this study of LERC performances can be applied to studies concerning the turnover rate estimator proposed by Nichols et al. (1998a) as the turnover is the probability that a species selected at random and at a given time period j (j being the most recent selection event) is locally a new species, and it is calculated by using local extinction rate data in reverse time order (Nichols et al. 1998a). Similarly, the results presented concerning temporal changes can be applied by analogy to spatial analyses (Nichols et al. 1998b). Indeed, the local extinction rate represents either the probability of species going extinct between two sampling events or the probability that a species found in one location is not found elsewhere (species co-occurrence). For example, to study the impact of diversity fragmentation, we can compare species richness and determine the proportion of species found in two distinct landscapes (Cam et al. 2000). It is also possible to test whether species composition in the fragmented landscape differs from the non-fragmented landscape. Indeed, if the probabilities of species co-occurrence do not differ from one (local extinction rate complement and turn over complement), we cannot reject the possibility that both landscapes present a similar species composition.

We showed that the bias induced by biological factors, which cannot be controlled for, such as species number, heterogeneity between the species in detection probability and extinction and the covariance effect, is relatively weak. Interestingly, a biological bias such as the uncontrollable covariance effect improves the estimation for small sampling efforts, without inducing a supplementary overestimation when these sampling efforts are high.

The most important factor affecting the performance of the estimator of the LERC is sampling effort, which can be increased by a larger number of occasions and/or amount of time per occasion, and by the quality of detection at each occasion. To obtain an acceptable performance of the LERC jackknife estimator, the minimum sampling effort must be a combination of a number of occasions and detection at each occasion (time and quality) leading to a detection probability at the scale of the primary sampling session higher than 50%. In this study we highlighted that the number of occasions is the most important factor that affects the performance of the LERC estimator. In the case of a low number of occasions, especially if the community is to be closed over the secondary sampling sessions, the effort could be focused on the quality of sampling at each occasion. For bird communities sampled via points counts during which all birds seen and heard at a stop during a fixed time observation period are recorded (e.g. Breeding Birds Survey), occasions can be either temporal or spatial replicated sampling of the studied community (Nichols and Conroy 1996). The simulation results provided in this paper, combined with empirical information from the literature and a specific pilot study tailored to the particular situation at hand, should thus help deciding how to allocate sampling efforts in a particular situation. A particular consideration has to be made to the trade off between the number of sampling occasion and their intensity (e.g. time spent for each point count), while considering the assumption of community closure. The assumption of community closure is important to consider carefully when using close-community estimators although one has to be practical; it should notably be noted that in some instance, the estimators are robust to violations of this assumption (Kendall 1999) and that in most cases where simple counts are used to characterize communities, such an assumption is anyway made implicitly.

In the field, all species are rarely detectable, so we recommend taking into account the species detection probability while estimating specie richness and vital rates responsible for community changes, such as extinction and turnover rates. It is possible to use other closed capture models (Otis et al. 1978), or others non-parametric methods (reviewed by Bunge and Fitzpatrick 1993, Lee and Chao 1994, Pledger 2000) to estimate species richness or to estimate similarity of specie composition (Chao et al. 2005). Several studies have compared the performance of species richness estimation methods (Smith and Van-Belle 1984, Palmer 1990, 1991, Baltanas 1992, Mingoti and Meeden 1992, Colwell and Coddington 1994, Chazdon et al. 1998), and concluded that the jackknife estimator generally performs well, frequently better than the other estimators. If no capture–recapture models fit the data, Nichols et al. (1998a) recommend the use of the robust jackknife estimator anyway. The approach to estimate species richness and vital rates responsible for spatial and/or temporal community changes proposed by Nichols et al. (1998a, 1998b), and their variance and confidences intervals, provides a simple methodological framework for studies of ecological communities.

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