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Exploring mark–resighting–recovery models to study savannah tree demographics

G. Lahoreau, J. Gignoux & R. Julliard

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Abstract

Exploring mark–resighting–recovery models to study savannah tree demographics.— Despite their sessile nature, juvenile trees in savannah ecosystems are not always easy to encounter. Here, we evaluate the applicability to plants of the remedy of choice in animal studies: capture–recapture modelling. The plant equivalents, tagging and resighting, were carried out in 7 censuses, involving 4,145 juvenile trees of 8 dominant savannah species. Using models with joint analysis of live and dead encounters, the resighting probabilities averaged 0.88 ± 0.15 and 0.92 ± 0.10 for seedlings and resprouts respectively; while dead recovery probabilities averaged 0.71 ± 0.25 for all age–classes. An *ad hoc* method that did not take into account encounter probabilities yielded biased survival estimates compared with estimates obtained using the mark–resighting–recovery approaches. This bias was observed even at high encounter probabilities, and we recommend therefore capture–recapture models where plant encounter is less than one. Finally, survival probabilities estimated by models based only on live or on dead data might both differ and be less accurate than estimates based on combined data. This highlights the advantages of models with joint analysis of live and dead encounters even the value of site fidelity is one.

Key words: Plant, Encounter, Survival, Capture–recapture model, Recovery data, Savannah.

Resumen

Exploración de los modelos de marcaje–reavistaje–recuperación para estudiar la demografía de los árboles de sabana.— Pese a su naturaleza sésil, los árboles jóvenes no siempre resultan fáciles de hallar en los ecosistemas de sabana. En el presente trabajo se evalúa la modelización de captura–recaptura, tan utilizada en estudios de animales, para su aplicación en los estudios de plantas. El equivalente al marcaje y reavistamiento para las plantas, se llevó a cabo a lo largo de siete censos, con un total de 4.145 árboles juveniles de ocho especies de la sabana dominantes. Mediante el empleo de análisis conjuntos de hallazgos de individuos vivos y muertos, las probabilidades de reavistamiento medias fueron de $0,88 \pm 0,15$ y $0,92 \pm 0,10$ para las plántulas y los rebrotes, respectivamente, mientras que el promedio correspondiente a las probabilidades de recuperación de individuos muertos fue de $0,71 \pm 0,25$ para todas las clases de edad. Un método especialmente diseñado que no tenía en cuenta las probabilidades de recaptura dio unas estimaciones de supervivencia sesgadas, en comparación con las estimas obtenidas utilizando las aproximaciones basadas en el marcaje–reavistamiento–recaptura. Este sesgo aparecía incluso con altas probabilidades de recaptura, por lo que recomendamos los modelos de captura–recaptura en los que la probabilidad de encontrar la planta es menor de uno. Por último, las probabilidades de supervivencia estimadas mediante los modelos basados únicamente en datos de plantas vivas o muertas pueden tanto diferir como ser menos precisas que las estimas basadas en datos combinados. Esto realza las ventajas de los modelos que emplean análisis conjuntos de hallazgos de plantas vivas y muertas, aun cuando el valor de la fidelidad al emplazamiento sea uno.

Palabras clave: Planta, Hallazgo, Supervivencia, Modelo de captura–recaptura, Datos de recuperación, Sabana.

G. Lahoreau & J. Gignoux, Lab. "Fonctionnement et Evolution des Systèmes Ecologiques", Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris Cedex 05, France.— R. Julliard, Lab. "Biologie de la Conservation", Muséum National d'Histoire Naturelle, CRBPO, 55 rue Buffon, 75005 Paris, France.

Introduction

Capture–recapture (CR) models were initially developed to estimate abundance, and later demographic parameters of animal populations, by overcoming the problem that not all animals in a sampling unit can be followed from one census to another (e.g. Bailey, 1952; Brownie et al., 1985; Pollock et al., 1990; Lebreton et al., 1992; Williams et al., 2001).

Although plants are sessile organisms, they might also suffer similar problems of detectability, and CR models have consequently been applied recently to plant populations. Small or non-flowering plants might be difficult to detect for example, living in grass or other ecosystems where they are surrounded by dense vegetation. Kery & Gregg (2003) have shown through a double-observer survey and a closed population CR model that detectability of the vegetative stages of the orchid *Cleistes bifaria* in meadow was just 0.82. Another problem is that plants that have periods of dormancy where they produce no aboveground structures might go undetected.

The Mead's milkweed, *Aclepias meaddi*, presents both these problems of detection. Its detectability has been estimated to be as low as 0.25 in a four-year study carried out in a U.S. prairie (Alexander et al., 1997). The use of a closed population CR model avoided underestimating the population size of this rare plant (Alexander et al., 1997). Slade et al. (2003) extended this study using a larger data set and an open population CR model, taking into account the possibility that some individuals might have died during the study period.

Where all non-dormant plants can be detected, CR models appear very promising to study dormancy because they yielded bias-free estimates of demographic parameters, including dormancy periods (Shefferson et al., 2001; Kery & Gregg, in press). In this case, the probability of dormancy (d) has been defined as the complement of the recapture probability (p): $d = 1 - p$. CR models have been used to demonstrate that dormancy probabilities are strongly correlated to weather covariates such as number of frost days (Shefferson et al., 2001) and precipitation during the previous spring (Kery & Gregg, in press).

In the present study of a humid African savannah in Côte d'Ivoire, similar detection problems were experienced, with it being impossible to track every individual juvenile tree. Savannah are defined as ecosystems where trees and grass coexist in the same area. In humid savannahs, fire is considered to be the main factor that limit abundance of trees, mainly because it burns juvenile trees growing within the flammable grass layer (e.g. Brookman–Amissah et al., 1980; San Jose & Farinas, 1983; Scholes & Archer, 1997; Gignoux et al., 1997). Few studies, however, have estimated juvenile survival probabilities in the field and in particular those of seedlings (Hochberg et al., 1994; Hoffman & Solbrig, 2003; House et al., 2003).

To estimate survival probabilities of juveniles in savannah trees, censuses were conducted in permanent plots every six months from June 1991 to July 1994. Despite intensive searches, not all juvenile trees were detected on each census, as they were often hidden by tall dense grass which exceeded 2 m in height from August to December (fig. 1). Moreover, because savannah trees are deciduous, it was not always possible to determine if they were alive or dead during censuses in December, which is at the end of the humid season. To avoid bias in survival estimates (Kery & Gregg, 2003), a capture–recapture approach is therefore appropriate. As the plant censuses provided information on both live and dead encounters, combined mark–resighting–recovery (MRR) models can be used. The theory for MRR models was initially developed by Burnham (1993) and then extended by Catchpole et al. (1998) to incorporate age effects. As MRR models allow estimation of survival probabilities with greater precision and little bias from emigration, they are increasingly used to study populations of birds (Szymczak & Rexstad, 1991; Catchpole et al., 1998; Frederiksen & Bregnballe, 2000; Blums et al., 2002; Francis & Saurola, 2002), mammals (Catchpole et al., 2000), turtles (Bjorndal et al., 2003; Seminoff et al., 2003) and also gastropods (Catchpole et al., 2001).

In this paper, (i) resighting, recovery and survival probabilities for juvenile trees of eight savannah species are estimated using MRR models; (ii) survival probabilities estimated in this way are then compared with those obtained using an *ad hoc* method which does not take encounter probabilities into account; and (iii) survival probabilities estimated using MRR models, and their precision, are also compared with those estimated by methods using data only from live resightings or on dead recoveries.

Materials and methods

Tree censuses in a humid savannah

The study was conducted in Guinean savannah at the Lamto research station in Côte d'Ivoire (06° 13' N, 05° 02' W). These savannahs are regulated by fires which occur annually during the January dry season (Abbadie et al., in press).

High rainfall, 1200 mm annually on average, means that the standing crop of grass can reach 1000 g·m⁻² at the end of the growing season. But grass production is strongly affected by the presence of trees, however, and be almost zero under clumps of trees (Abbadie et al., in press).

From 1991 to 1994, seven plant censuses were conducted six months apart in four 50 × 50 m plots at the height of the wet season (June 1991, June 1992, July 1993 and July 1994) and at the beginning of the dry season (December 1991, November 1992 and December 1993). This allowed estimates of survival probabilities both during fire and grow-

ing seasons. To simplify analyses, all censuses were considered to have been done at exactly 6-month intervals, in June and in December.

During the first census, the position of more than 5,000 trees, including tiny seedlings, was marked with a fire-resistant iron flag attached to a 50 cm stake (fig. 1). Subsequent censuses counted not only plants that had been tagged already, but also new individuals (around 1,000 per year). Trampling of grass tufts was avoided by walking between them, as grass affects the growth of juvenile trees through competition for light, water and nutrient (Scholes & Archer, 1997).

At each census, data were recorded on species, height and demographic state—seedlings (recently germinated), resprouts (more than one year old but with no perennial stem), and adult trees (with a perennial trunk)—age of stems (annual/perennial) was easily determined by the presence/absence of fire scars. Dead plants—flag—but no plant in the vicinity—were also tracked.

If the viability of an individual could not be determined, because of the absence of leaves on the stem, it was recorded as being leafless state and for the purpose of analyses was considered as in an "un-encountered" state, regardless of its state in the following census.

Four thousands one hundred forty five individuals were studied from eight dominant Savannah tree species: *Annona senegalensis* (Annonaceae, 917 individuals), *Bridelia ferruginea* (Euphorbiaceae, 702), *Crossopteryx febrifuga* (Rubiaceae, 234), *Cussonia arborea* (Araliaceae, 747), *Piliostigma thonningii* (Cesalpiniaceae, 317), *Psorospermum febrifugum* (Clusiaceae, 303), *Pterocarpus erinaceus* (Fabaceae, 354), *Terminalia shimperiana* (Combretaceae, 571).

From censuses to encounter histories

Encounter histories were generated from individual census data (table 1). As resprout survival is known to be size-dependent (Gignoux et al., 1997; Hoffman & Solbrig, 2003), all resprouts were classified into one of 3 age-classes: one-year old (R_1), two-year old (R_2) and three-year or older (R_3) resprouts.

Resprouts found in years subsequent to 1991, which had not previously been recorded as seedlings (S), were assumed to be R_1 . Resprouts found during the first census were assumed to be R_3 , given that their exact age was not known and that R_1 and R_2 should be a minority of this population. The proportion of the different resprout age-classes in July 1994 gives an estimate error: between 3% and 39% of resprouts were younger than three-years old.

If a resprout became an adult, it was nonetheless still considered as resprout as integrating an adult tree state would have required a multi-state CR model.

Individuals not recorded in one census, but found dead in a subsequent one (i.e., flag detected but no plant in the vicinity) were labelled as delayed recoveries (Catchpole et al., 2001): the timing of death



Fig. 1. Resprout of *Bridelia ferruginea* marked with a tagged steel stake in the savannah at the Lamto research station, Côte d'Ivoire.

Fig. 1. Rebrote de *Bridelia ferruginea* identificado mediante una estaca de acero marcada en la sabana en la estación de investigación de Lamto, Costa de Marfil.

could not be determined accurately. In this case, the dead recovery was omitted (see the last case in table 1) to prevent the bias that would be caused if such individuals were considered to have died during the last observation period—this concerned 7.7% of all plants.

For each tree species, the seven censuses allowed estimation of survival probabilities for six time periods for seedlings and for R_3 , four for R_1 and only two for R_2 .

Mark-resighting-recovery (MRR) models

The parameters of the MRR model are: ϕ , the apparent survival probability, S , the true survival probability, p , the resighting probability, r , the recovery probability and F , the fidelity probability.

True and apparent survival ϕ are linked by the fidelity parameter as $\phi = S \times F$. Originally, site fidelity was defined as that probability an individual would remain in the study area (Burnham, 1993), on

Table 1. Examples of encounter history provided by the seven censuses made from June 1991 to July 1994 with: S. Seedling; R₁. One-year old resprout; R₂. Two-year old resprout; R₃. Three-year or older resprout; T. Adult tree; D. Dead individual; 0. Un-encountered individual.

Tabla 1. Ejemplos de la relación de hallazgos proporcionados por los siete censos realizados entre junio de 1991 y julio de 1994 con: S. Plántula; R₁. Rebrote de un año de edad; R₂. Rebrote de dos años de edad; R₃. Rebrote de tres años de edad o más; T. Árbol adulto; D. Individuo muerto; 0. Individuo no encontrado.

Encounter history	Observation
SSD0000	Seedling found in June 1991 and in December 1991, found dead in June 1992
000SR ₁ 00	Seedling found in December 1992, hence not detected at that stage in June 1992. Found again in June 1993 but never encountered after.
00R ₁ R ₁ R ₂ 0R ₃	Resprout found the first time in June 1992, expected to having been missed on seedling state in 1991 and so to be 1-year old. Seen every following year excepted in December 1993
R ₃ R ₃ R ₃ R ₃ R ₃ R ₃	Resprout found in June 1991, assumed to be 3-year old or older resprout. Found alive during all subsequent censuses.
R ₃ R ₃ R ₃ R ₃ TTT → R ₃ R ₃ R ₃ R ₃ R ₃ R ₃	Resprout which became an adult tree in June 1993, considered to stay in resprout state
S0D0000 → S000000	Seedling found in June 1991, not found in December 1991 but found dead in June 1993. In such case, we omitted the delayed recovery.

the assumption that resightings take place locally, while recoveries can take place anywhere. On this basis, F would equal one for plants. Recently, Frederiksen (unpublished work) proposed that F might be more appropriately considered as a correction factor which allows unbiased estimation of survival when p or r are highly heterogeneous among individuals. To test this, we allowed F to vary with time; F was invariably estimated at one, suggesting little parameter heterogeneity. As a result, we fixed the value of F as one.

In animal studies, dead individuals are usually found by the general public, often hunters and members of the recovery parameter r has therefore been defined as incorporating both the probabilities of finding a dead individual and of reporting its band (White & Burnham, 1999; Otis & White, 2002). In plant censuses, the demographers record all individuals found dead so that the probability of tag reporting equals one, and r represents the probability of finding a dead plant.

As we were interested in ascertaining survival probabilities for each species, we developed a general model for each incorporating all possible effects: (1) time and age-dependence for survival probabilities; (2) time and age-dependence for resighting probabilities (which might be dependent on individual size, itself related to age); and (3) time-dependence for recovery probabilities (age dependence was considered irrelevant, as the probability of finding only a flag should be identical for all dead individuals).

The general model was therefore:

$$S(a4-t/t/t)p(a4-t/t/t)r(t)F \quad (1)$$

where $a4$ means that 4 age-classes were considered —namely S, R₁, R₂, and R₃— t means time-dependence and therefore $a4-t/t/t$ means time-dependence for each of the 4 age-classes (Cooch & White, 1999).

We created the general models with the "Burnham model" using the MARK software programme (White & Burnham, 1999), which expands upon the MRR theory of Burnham (1993) to allow age-dependent parameters. Age-classes were coded into two groups: the first composed of individuals marked in a seedling, and the second of those marked as resprouts with the assumption that resprouts marked in 1991 started as R₃ and those in 1992 and 1993 as R₁.

For each species, we investigated the fit of the global model to the data using the MARK bootstrap procedure, with simulation of 100 data sets and calculation their deviances (White & Burnham, 1999). If the deviance of the global model did not fall within that of the 100 simulated deviances, the global model was not a good fit (White & Burnham, 1999).

The global model did not fit the data ($P < 0.01$) in any tree species except *Terminalia shimperiana*, and the significance of the fit on the latter was itself borderline ($P = 0.06$). This indicated either overdispersion of the data or failure of the model to account for the data

structure (Lebreton et al., 1992; Burnham & Anderson, 1998). In animal count data, overdispersion is very common and occurs when some assumptions of CR models, such as independence or homogeneity of parameters are violated in some groups of individuals (Lebreton et al., 1992; Burnham & Anderson, 1998). In plants, overdispersion of the data is likely given that their frequently clumped distribution could result in non-independent capture probabilities (Kery & Gregg, 2003).

Assuming the lack of fit was due to overdispersion, we therefore calculated a variance inflation factor (\hat{c}) as the ratio of our model deviance to the mean of the 100 simulated deviances with the MARK bootstrap procedure (White & Burnham, 1999). The variance inflation factors for the eight species range from 1.34 to 2.98 (table 2). We then used the corrected Quasi-Akaike Information Criterion, QAIC_c, which incorporates corrections for small sample and overdispersion to select among models (Burnham & Anderson, 1998). The best approximating model was that with the lowest QAIC_c value, but models with QAIC_c differences < 2 should also be considered as possible candidate models. In such cases, we chose the model with the highest number of parameters, to incorporate all potential biological effects.

Several reduced-parameter models were considered. First, the age-dependence of the resighting probabilities was reduced by clumping age-classes. Models were constructed with only three age-classes, by clumping two resprout age-classes together (R_1 and R_2 or R_2 and R_3), with only two age-classes (seedlings and resprouts, with all resprout age-classes grouped), and finally with no age-effect.

Second, models were developed allowing p and r to be dependent on season without year variation, or constant through years and seasons. It was assumed that p might be higher in June than in December, when leaf fall occurs. But as previous studies have shown that the time and duration of leaf fall vary considerably from year to year (Hopkins, 1970; Menaut & Cesar, 1979), models were also tested where p was constant in June but year-dependent in December.

Direct survival (DS) estimation

An *ad hoc* analysis was used, named direct survival (DS) estimation, which assumed that the level of encounter equalled one (i.e. all live and dead individuals were found). Only data composed of individuals alive at time $i-1$ and found dead or alive at time i was used to calculate survival rate at time i . This therefore required no assumptions about internal or external zeros.

In such analyse, the encounter history "SOR₁R₁000" was not used to estimate the seedling survival rate between time 1 and 2 or between time 4 and 5, but was used to estimate the R_1 survival rate between time 3 and 4. As in the MRR models, information from delayed recoveries was not used.

Table 2. Variance inflation factor (\hat{c}) of the global model calculated with the bootstrap procedure of the program MARK for each of the eight savannah tree species.

Tabla 2. Factor de inflación de la varianza (\hat{c}) del modelo global calculado mediante el procedimiento bootstrap del programa MARK para cada una de las ocho especies de árboles de sabana.

Tree species	\hat{c}
<i>Annona senegalensis</i>	2.02
<i>Bridelia ferruginea</i>	1.90
<i>Crossopteryx febrifuga</i>	2.22
<i>Cussonia arborea</i>	2.98
<i>Piliostigma thonningii</i>	1.87
<i>Psorospermum febrifugum</i>	1.42
<i>Pterocarpus erinaceus</i>	1.63
<i>Terminalia shimperiana</i>	1.34

The survival rate was then simply calculated as the fraction of survivors as is usually done in plant studies (e.g. Garnier & Dajoz, 2001; Hoffman & Solbrig, 2003).

The underlying assumption of the DS estimation was therefore that the proportion of alive/dead individuals was the same for encountered and unencountered plants and that resighting and recovery probabilities were therefore identical. This assumption was hypothesized to be false, as live plants were easier to find than dead ones (field observation).

Bias was estimated as the difference between the survival rates estimated by the DS (S_{DS}) and MRR (S_{MRR}) methods:

$$\text{Bias} = S_{DS} - S_{MRR}$$

Bias was tested to determine if it was negatively correlated to the percentage of individuals encountered, defined as the proportion of individuals alive at time $i-1$ and found dead or alive at time i .

All statistics were done using SAS software (SAS Institute, 1990).

Comparison with alive or dead models

Following comments of Burnham (1993) and studies of Catchpole et al. (1998) and Francis & Sauro (2002), results from MRR were compared to those from models based only on live resightings (e.g. Lebreton et al., 1992) or on

Table 3. Selected dependence for resighting (p) and recovery (r) probabilities for the eight savannah tree species with initially four age-classes considered: S. Seedlings; R_1 . One-year old resprouts; R_2 . Two-year old resprouts; R_3 . and three years or older resprouts; $a3(S, R_1, R_2, R_3)$. The selected parameter were 3 age-classes dependent with R_1 and R_2 clumped; $a3(S, R_1, R_2, R_3)$. The selected parameter were 3 age-classes dependent with R_2 and R_3 clumped; $a2(S, R_1, R_2, R_3)$. The selected parameter were 2 age-classes (seedlings vs resprouts); t . Probabilities were time-dependent; c . Constant over time; *season*. Probabilities were different in June and in December; and $Dec(t)June(c)$. Parameters were time-dependent in December but constant in June.

Tabla 3. Dependencia seleccionada con respecto a las probabilidades de reavistaje (p) y recuperación (r) para las ocho especies de árboles de sabana, inicialmente con cuatro clases de edad consideradas; concretamente: S. Plántulas; R_1 . Rebrotos de un año de edad; R_2 . Rebrotos de dos años de edad; R_3 . Rebrotos de tres años de edad o más; $a3(S, R_1, R_2, R_3)$. El parámetro seleccionado comprendía tres clases de edad dependientes, con R_1 y R_2 agrupados; $a3(S, R_1, R_2, R_3)$. El parámetro seleccionado comprendía tres clases de edad dependientes, con R_2 y R_3 agrupados; $a2(S, R_1, R_2, R_3)$. El parámetro seleccionado comprendía dos clases de edad (plántulas frente a rebrotos); t . Las probabilidades dependían del tiempo; c . Constante a lo largo del tiempo; *season*. Las probabilidades diferían en junio y diciembre; y $Dec(t)June(c)$. Los parámetros dependían del tiempo en diciembre, pero se mantenían constantes en junio.

Tree species	p	r
<i>Annona senegalensis</i>	$a3(S, R_1, R_2, R_3)-t/season/t$	t
<i>Bridelia ferruginea</i>	c	t
<i>Crossopteryx febrifuga</i>	<i>season</i>	t
<i>Cussonia arborea</i>	$a2(S, R_1, R_2, R_3)-t/Dec(t)June(c)$	t
<i>Piliostigma thonningii</i>	$a3(S, R_1, R_2, R_3)-season/season/season$	c
<i>Psorospermum febrifugum</i>	$a3(S, R_1, R_2, R_3)-season/t/t$	t
<i>Pterocarpus erinaceus</i>	$a3(S, R_1, R_2, R_3)-t/t/t$	<i>season</i>
<i>Terminalia shimperiana</i>	$a2(S, R_1, R_2, R_3)-Dec(t)June(c)/t$	t

dead recoveries (e.g. Brownie et al., 1985). Unlike animal studies (Francis & Cooke, 1993), the resighting models allowed estimation of survival probabilities free from emigration bias, as plants do not move ($F = 1$).

For each model and making the same assumptions as in the combined analysis the following general models were considered:

Live encounters model: $S(a4-t/t/t)p(a4-t/t/t)$

Dead recoveries model: $S(a4-t/t/t)r(t)$

Using the bootstrap procedure (White & Burnham, 1999), the live sightings model appeared to fit the data for four tree species ($0.04 < P < 0.17$), and the dead recoveries models appeared to fit for six ($0.03 < P < 0.64$). Nevertheless, the variance inflation factors were quite similar to those calculated using MRR models (live models: $1.19 < \hat{c} < 2.58$; dead models: $0.88 < \hat{c} < 2.50$). As in the MRR approach, submodels were also defined and model selection was based on QAIC_c values.

Results

Resighting and recovery probabilities

The most parsimonious MRR models indicated that resighting probabilities, p , were (table 3): (1) similar for all age-classes in *Bridelia ferruginea* and *Crossopteryx febrifuga*; (2) different between seedlings and resprouts but not between resprout age-classes in *Cussonia arborea* and *Terminalia shimperiana*; and (3) different for 3 age-classes with R_1 and R_2 clumped (*Pterocarpus erinaceus*) or with R_2 and R_3 clumped (*Annona senegalensis*, *Piliostigma thonningii* and *Psorospermum febrifugum*).

Depending on species and age-classes, p was either constant, dependent on season (with probabilities constant in December or not), or dependent on time (table 3). Average resighting probabilities across species were 0.88 ± 0.15 for seedlings, 0.92 ± 0.08 for R_1 , 0.89 ± 0.11 for R_2 and 0.94 ± 0.11 for R_3 .

Recovery probabilities were time-dependent for all species, with the exception of *Piliostigma*

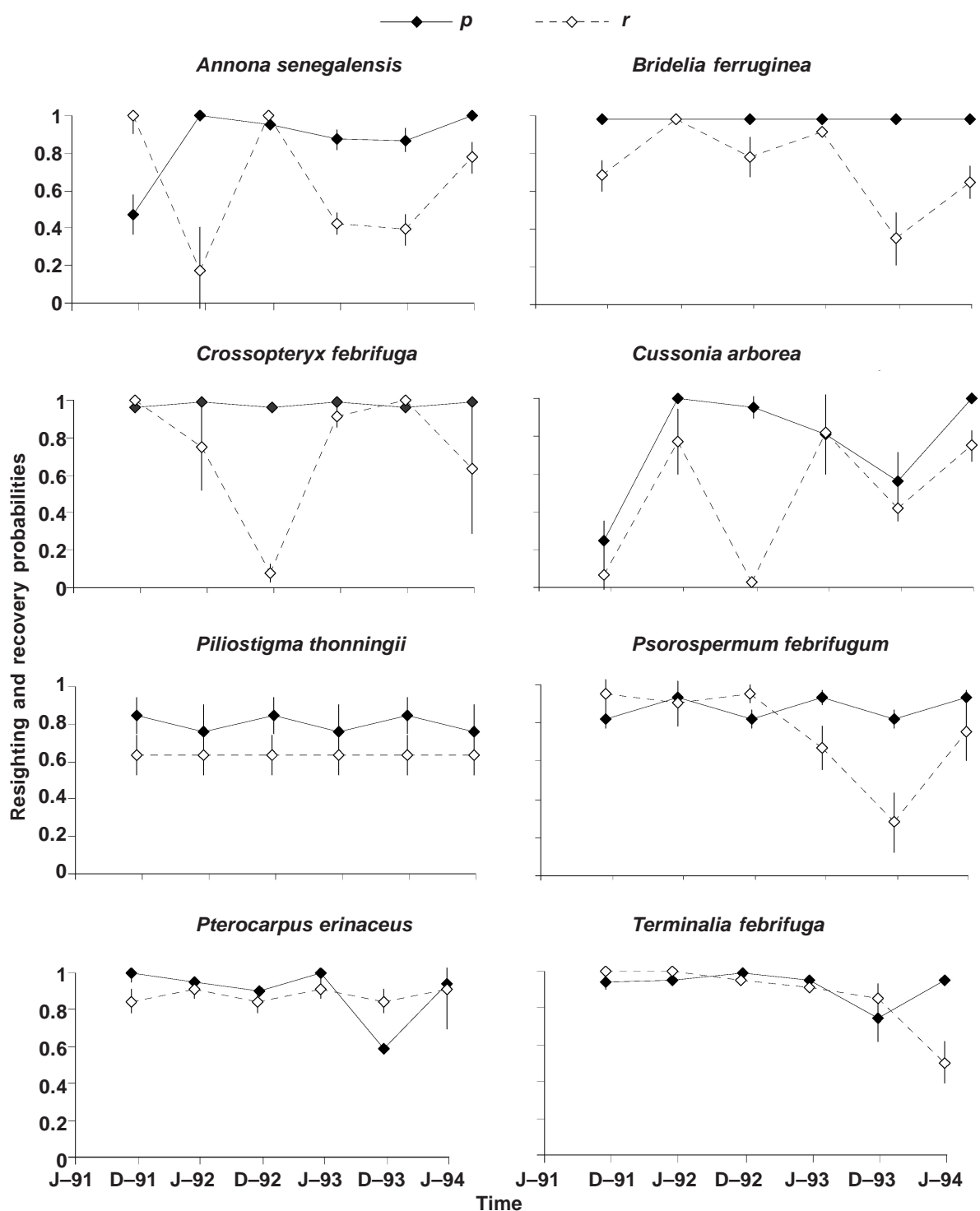


Fig. 2. Resighting (p) and recovery (r) probabilities for the seedlings estimated by the mark-resighting-recovery models for the eight savannah tree species (with standard error), as estimated by models listed in table 3: J. June; D. December.

Fig. 2. Probabilidades de reavistaje (p) y recuperación (r) con respecto a las plántulas estimadas mediante los modelos de marcaje-reavistaje-recuperación para las ocho especies de árboles de sabana (con error estándar), según lo estimado por los modelos especificados en la tabla 3: J. Junio; D. Diciembre.

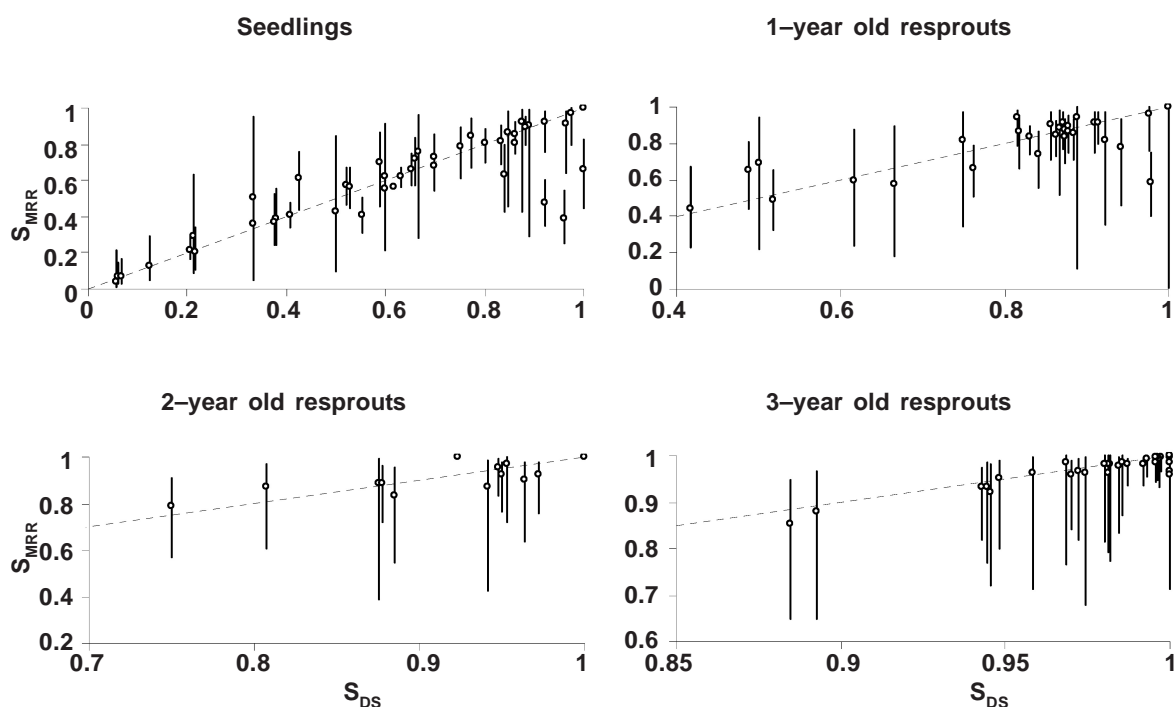


Fig. 3. Comparison of the survival probabilities obtained by direct survival estimation (S_{DS}) (confidence limits not shown) and by the mark–resighting–recovery model (S_{MRR}) (with 95% confidence intervals). All survival probabilities estimated per each age–classes for the eight savannah tree species are represented, i.e. 48 for seedlings and for 3–year or older resprouts, 32 for 1–year old resprouts and 16 for 2–year old resprouts. The dashed lines represent the line $x = y$.

Fig. 3. Comparación de las probabilidades de supervivencia obtenidas mediante la estimación directa de supervivencia (S_{DS}) (límites de confianza no indicados) y mediante el modelo de marcaje–reavistaje–recuperación (S_{MRR}) (con intervalos de confianza del 95%). Se representan todas las probabilidades de supervivencia estimadas para cada clase de edad de las ocho especies de árboles de sabana; es decir, 48 para las plántulas y para los rebrotes de tres años de edad o más; 32 para los rebrotes de un año de edad y 16 para los rebrotes de dos años de edad. Las líneas discontinuas representan la línea $x = y$.

thoningii and *Pterocarpus erinaceus* (table 3). Values varied widely among species, but the average r was 0.71 ± 0.25 . Temporal variation was generally greater than variation in resighting probabilities, with recovery probabilities ranging from 0.25 to 1 (fig. 2). In more than 77% of estimates, recovery probabilities were lower than resighting probabilities.

Bias in survival probabilities

Across species, based on MRR, the survival probabilities averaged 0.60 ± 0.23 for seedlings, 0.80 ± 0.16 for R_1 , 0.93 ± 0.07 for R_2 and 0.98 ± 0.23 for R_3 (fig. 3).

To compare survival probabilities between the MRR model (S_{MRR}) and the DS estimation (S_{DS}), all the individual period–specific survival probabilities

were estimated for all tree species resulting in a total of 48 survival probabilities (6 time periods \times 8 species) for seedlings, 32 for R_1 , 16 for R_2 and 48 for R_3 (fig. 3). Estimates from DS models were biased almost as much positively as negatively compared with the MRR approach; but higher bias estimates were mainly positive. The DS approach overestimated the survival probabilities up to 0.57 for seedlings, up to 0.39 for R_1 , up to 0.07 for R_2 and up to 0.04 for R_3 (fig. 4).

The magnitude of bias in absolute values was negatively correlated with the percentage of individuals encountered in seedlings ($P < 0.001$; $R^2 = 42\%$) and in R_1 ($P = 0.008$; $R^2 = 32\%$), but in R_2 ($P = 0.84$) and in R_3 ($P = 0.97$).

The apparent bias even where the percentage of encounters was 100%, resulted from the way the percentage of encounters and S_{DS} were calculated.

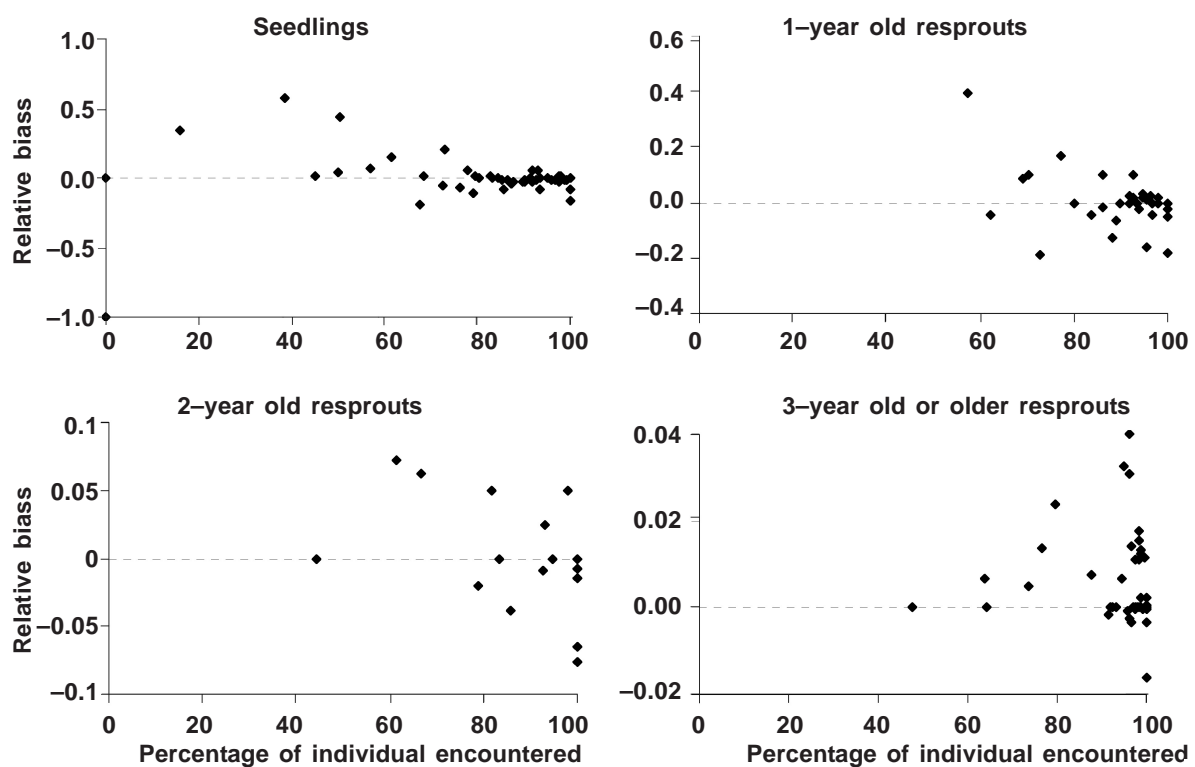


Fig. 4. Relative bias in survival probabilities (Bias = $S_{DS} - S_{MRR}$) as a function of the percentage of individual encounters with S_{DS} , the survival probabilities obtained by the direct survival estimation and S_{MRR} by the mark-resighting-recovery model. Dashed lines represent the line $x = 0$.

Fig. 4. Sesgo relativo en las probabilidades de supervivencia (Sesgo = $S_{DS} - S_{MRR}$), expresado como una función del porcentaje de hallazgos individuales con S_{DS} , las probabilidades de supervivencia obtenidas mediante la estimación directa de supervivencia y S_{MRR} mediante el modelo de marcaje-reavistaje-recuperación. Las líneas discontinuas representan la línea $x = 0$.

Indeed, encounter histories such as "R₃00R₃R₃R₃" were not used to calculate the percentage of individual encounters and S_{DS} between time 2 and 3 but were used to estimate S_{MRR} .

Alive, dead and combined models

The resighting models did not always permit estimation of survival probabilities for the last period due to the selected model structure. The value and the precision of the survival probabilities using only resighting data were very similar to those obtained using the MRR models (fig. 5).

For recovery-only models, all survival probabilities could be estimated, as time-dependence of r was never selected (results not shown). Many survival probabilities based only on recovery data differed from those obtained using MRR models. The precision of the survival estimates from recovery models was also frequently much lower (i.e. higher standard error, fig. 5).

Discussion

MRR models in the study of plant populations

MRR models were applied here to plant populations and found to work well. Their use might thus increase in the future, as plant censuses often record both live and dead individuals without always detecting every individual on every visit.

Variance inflation factors in the general model of the eight savannah tree species ($1.34 < \hat{c} < 2.98$) were quite similar to those of animal populations. Overdispersion is likely to occur in plants (Kéry & Gregg, 2003), and might be even more frequent and substantial in savannahs due to the spatial heterogeneity of the ecosystem ranging from open grass areas to dense tree clumps. The high value of $\hat{c} = 2.98$ for *Cussonia arborea* reflect the interdependence of survival probabilities for its seedlings, which unlike those of the other species observed, aggregate under the mother tree crown.

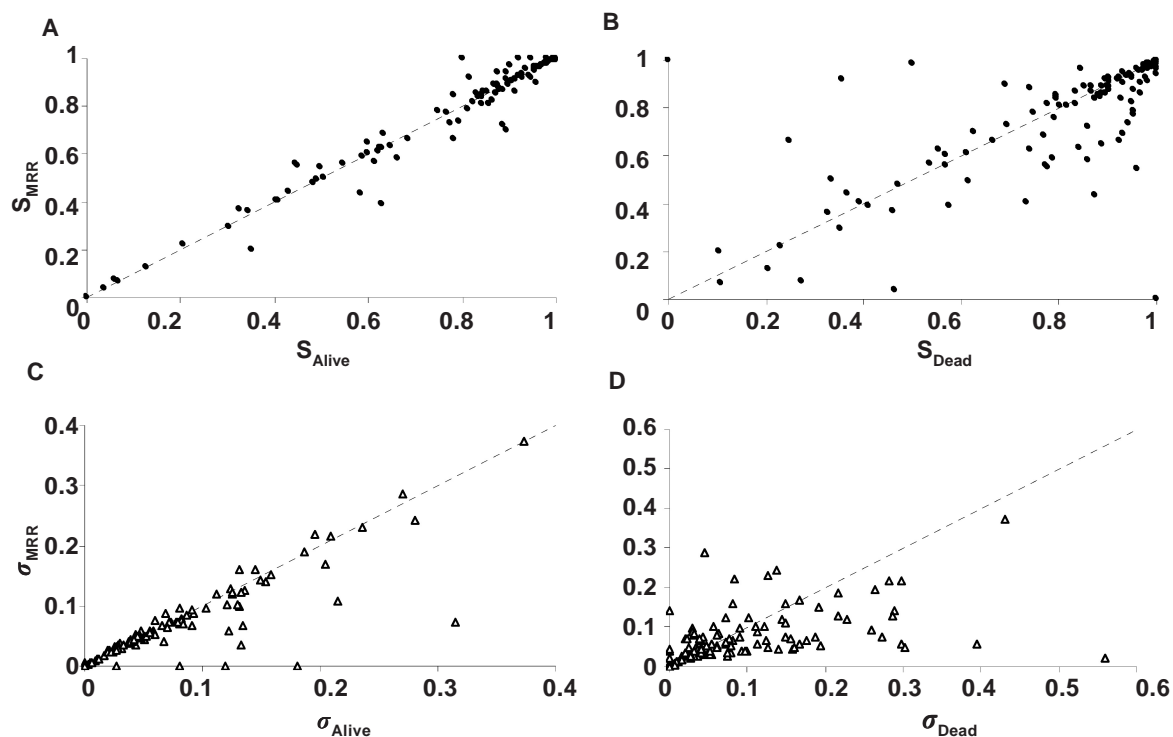


Fig. 5. 5A, 5B. Comparison between the survival probabilities estimated by the resighting-only models (S_{Alive}) and the recovery-only models (S_{Dead}) to these by the mark-resighting-recovery models (S_{MRR}). 5C, 5D. Comparison between the standard errors estimated by the resighting-only models (σ_{Alive}) and the recovery-only models (σ_{Dead}) to these by the mark-resighting-recovery models (σ_{MRR}). All survival estimates and their standard errors per time for all age-classes of the eight savannah tree species are represented. The dashed lines represent the line $x = y$.

Fig. 5. 5A, 5B. Comparación entre las probabilidades de supervivencia estimadas mediante los modelos de sólo reavistaje (S_{Alive}) y los modelos de sólo recuperación (S_{Dead}) y las tesis obtenidas mediante los modelos de marcaje-reavistaje-recuperación (S_{MRR}). 5C, 5D. Comparación entre los errores estándar estimados mediante los modelos de sólo reavistaje (σ_{Alive}) y los modelos de sólo recuperación (σ_{Dead}) y las tesis obtenidas mediante los modelos de marcaje-reavistaje-recuperación (σ_{MRR}). Se representan todas las estimaciones de supervivencia y sus errores estándar por tiempo para todas las clases de edad de las ocho especies de árboles de sabana. Las líneas discontinuas representan la línea $x = y$.

For the eight savannah tree species, the average $r = 0.71 \pm 0.25$ was lower than resighting probabilities in seedlings ($p = 0.88 \pm 0.15$) and in resprouts ($p = 0.92 \pm 0.10$) confirming the field impression that finding only a flag was more difficult than finding a flag and an associated plant.

Bias in survival estimates

Encounter probabilities less than 1.0 introduced bias into the survival probabilities as assumed by Kery & Gregg (2003), and could lead to misleading conclusions and predictions. Percentage of encounters was generally not a good predictor of the bias magnitude, suggesting that

CR models should be used even when encounter rates are high. Contrary to expectations, however bias was not consistently in the same direction.

For three-year or older resprouts, survival probabilities were close to 0.9 and the biases did not exceed 0.04. Nevertheless, such small differences might have a major impact on estimates of long-term survival probabilities and estimated population dynamics, as resprouts might remain in that state for decades before becoming adults or simply dying. For example, the probability for a resprout to survive 10 years (20 seasons) equals 0.82 if $S = 0.99$ (0.99^{20}) but only 0.35 if $S = 0.95$ (0.91^{20}).

Comparison between capture–recapture and recovery models

As observed by Catchpole et al. (1998) and Francis & Saurola (2002), survival probabilities estimated by models based only on live or only on dead encounters sometimes different from those estimated using combined models, and were generally less precise. Estimates from models with live sightings or dead recoveries alone were potentially more biased than MRR models. This was particularly true in recovery models. In plant censuses, dead individuals are, however, rarely recorded without there being information about live individuals.

Conclusion

Mark–resighting–recovery models are well-suited to retrospective analyses of existing and valuable historical datasets on plant ecosystems. In future experiments in savannah ecology, improvements in methodology such as electronic tagging of plants may ameliorate resighting and recovery, although field studies will, for the foreseeable future, often by necessity be conducted under onerous logistical conditions. A combination of improved techniques, combined with imaginative modelling, will provide a means to advance the study of tree dynamics in savannah ecosystems and enhance understanding of the factors limiting their distribution and abundance.

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