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Modeling unobserved variables in dendrochronological age structures improves inferences about population dynamics.

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Abstract

The loss of evidence poses a major challenge to historical ecology. For example, dendroecological studies aiming at relating tree establishment with past climate should consider the possibility that many plants might not survive to be recorded at the date of the study. A standard approach to deal with this data loss consists in fitting an exponential decay curve to the observed age structure and using the residuals of this fit as a proxy of tree establishment. Here we show that Hierarchical Bayesian analysis (HBA) where tree establishment is modeled as a latent variable can outperform the standard approach. We illustrate the use of HBA with a simulation study where the goal is to infer population dynamics from dendrochronological age-structures. Both methods are also used to analyze empirical data from expanding alder forests in northwestern Argentina. The simulation study showed that the standard approach underestimated the association between rainfall and tree establishment. The HBA was unbiased and had narrower uncertainty around estimates. In the empirical study, the HBA detected effects of rainfall on tree establishment, which were deemed not significant by the standard approach. Besides these advantages, the flexibility of HBA should allow the analysis of more complex (and realistic) models.

35

Keywords: Bayes, coverage, dendrochronology, hierarchical analysis, uncertainty, unobserved variable

38

39 **1. Introduction**

40 Historical ecology aims at reconstructing and depicting the environmental history of particular
41 ecosystems in order to understand their interactions with ecological agents and other factors in
42 the past. Thus, this discipline is informative for conservation, restoration and forecasting
43 potential consequences of climate and land use changes. The most important constraint that
44 historical reconstructions must deal with is the loss of evidence through time due to the natural
45 degradation of the record (Egan and Howell 2001). This loss poses a challenge for any study of
46 historic ecology because it reduces the reliability of reconstructions as time before present
47 increases, and hence it must be taken into account in order to interpret data from historical
48 records (Swetnam et al. 1999).

49

50 Dendrochronology is one of the most widespread methods used in historical ecology
51 (Schweingruber 1988). Dendrochronology is used to reconstruct different aspects of past
52 environments, such as climate (Briffa 2000), disturbance regime (Veblen et al. 1994), and
53 human activity (Haneca et al. 2009). Sometimes this technique is used to describe the age
54 structure of woody plants (e.g. Villalba and Veblen 1997; Miller and Halpern 1998; Carilla and
55 Grau 2010). Other studies aim at assessing the environmental factors that controlled tree
56 establishment in the past to understand the processes leading forest dynamics, which has
57 significant implications in the management and forecasting of forests affected by environmental
58 changes.

59

60 In many parts of the world forests are shifting their extent due to forest transition (forests expand
61 in areas where land use intensity is reduced, Rudel et al. 2005) or due to global warming (forests
62 move upwards or toward higher latitudes, Harsch et al. 2009). Under both scenarios the
63 dynamics of forests are likely to be affected by climate change, so accurate forecasting based on

64 historical evidence will be crucial for the implementation of adequate management policies
65 (Johnson et al. 1994). For example, alder montane forests of northwestern Argentina encroached
66 over adjacent grasslands during the 20th century (Grau 1985). An increase in regional rainfall
67 (Minetti and Vargas 1998) has been proposed as one of the causes of this expansion of forests
68 but, to our knowledge, no formal analysis has been performed.

69

70 The analysis of tree age structures generated through dendrochronological methods can be
71 helpful to understand the climate control on tree establishment. However, the effect of tree
72 mortality (and the consequent loss of information) in these assessments is usually overlooked or
73 handled deficiently. Different approaches have been proposed to deal with data loss in static age
74 structure analyses (e.g. Miller and Halpern 1998; Mast et al. 1999; Grau and Veblen 2000;
75 Wang et al. 2006; Danby and Hik 2007; Carilla and Grau 2010). Some studies do not take
76 mortality into account and consider that the observed frequency in each age class is a good
77 indicator of tree establishment in the corresponding time interval (e.g. Miller & Halpern 1998).
78 These studies use correlation analysis between age-class frequency and meteorological records
79 of the corresponding period of establishment to make inferences about climate control on tree
80 establishment (e.g. Miller and Halpern 1998, Wang et al. 2006). Other studies combine data of
81 living trees with that of dead logs to reconstruct past tree establishment (e.g. Mast et al. 1999).
82 This approach overcomes some of the problems arising from mortality, but it cannot be applied
83 in environments where dead logs decay rapidly or when their dating may be inaccurate (Danby
84 and Hik 2007). Another approach was used by Grau and Veblen (2000), who grouped observed
85 frequencies in 5 year age classes for 10 age structures of trees and performed a principal
86 component analysis assigning the first component to mortality (which was supported by a strong
87 correlation with calendar year) and used the 2nd and 3rd components to evaluate the relationships
88 with environmental factors. Alternatively, mortality rates from an independent source such as

89 permanent plots (e.g. Carilla and Grau 2010) can be used to estimate tree establishment from
90 observed age structures. In this approach mortality can be accurately measured, but it does not
91 take into account potential differences between populations. Moreover permanent plots usually
92 do not include all age classes and they have a limited time span. As these methods are based on
93 ad hoc assumptions their use is not universal. Yet, there exists a “standard method” based on
94 simple statistical analysis. This method fits a negative exponential curve to the age structure to
95 estimate the expected number of trees established at time t assuming constant mortality rates.
96 Sometimes, instead of a negative exponential, a power function is fitted to model age-dependent
97 mortality (Hett and Loucks 1976; Batllori and Gutiérrez 2008). The residuals of the curve are
98 anomalies that represent an indicator of tree establishment. So, climate control on tree
99 establishment is inferred by regressing these residuals against meteorological records (e.g.
100 Daniels and Veblen 2004; Gamache and Payette 2005; Danby and Hik 2007). This method
101 implies two steps, the estimation of mortality and the parameterization of the association
102 between establishments and climate. The proxy of establishment is based on a single estimate of
103 mortality so the error of the estimate of mortality is carried over to the next step reducing the
104 statistical power of the method.

105

106 In this study we propose the use of Hierarchical Bayesian Analysis (HBA, Clark 2005) to
107 explicitly deal with the different processes involved in population dynamics using a latent
108 variable to model the unobservable establishments in the past. To compare the proposed and the
109 standard methods we simulate forest dynamics with constant mortality and establishment
110 controlled by climate. We estimated the parameters of the emergent data with HBA and with the
111 standard method to assess their performance. We also used both methods to analyze empirical
112 data from *A. acuminata* dominated forests from a subtropical montane system.

113

2. Material and methods

2.1.A model for tree recruitment

In forest-grassland interfaces the seedling stage is considered the bottleneck for tree establishment so that environmental conditions during this stage constrain recruitment (Sankaran et al. 2004). For simplicity we assumed that water availability in year “ t ” is the only restriction to tree establishment (N_t) and that the association between rainfall (R_t) and tree establishment is linear (e.g. Daniels and Veblen 2004). The number of seedlings established at time t is modeled as a latent (unobserved) variable because usually it cannot be observed directly since establishments occurred in the past. The stochasticity in the number of establishments was modeled with a Poisson distribution, with intensity (λ_t) being a linear function of rainfall:

$$(eqn 1) N_t \sim Poisson(\lambda_t)$$

$$\lambda_t = \max(a + bR_t, 0)$$

where a is the expected number of establishments when rainfall is zero, and b is the increase in this expectation when there is a one unit raise in annual rainfall. Clearly, other formulations for this relationship are possible; a log-linear model could be used to naturally constraint λ to be positive or the relationship between establishments and rainfall could be modeled with some non-linear function. We used a linear model to make the comparison with the standard approach straightforward and eqn 1 was truncated at zero to avoid negative λ values.

Due to mortality, only some (if any) of the trees that were established at time t , would be present at the time of observations (t_{obs}) which we modeled with a Binomial distribution:

$$(eqn 2) O_c \sim Binomial(N_t, s_c)$$

$$s_c = \exp(-d(t_{obs} - t))$$

139

140 Here, O_c is the observed number of trees belonging to age class c . Age structure is a snapshot of
 141 a population at the sampling time (t_{obs}). Yet, inferences are referred to the establishment time t .
 142 The number of trees in each age class (O_c) is a fraction of those that recruited (N_t). The
 143 individual-level probability of surviving $t_{\text{obs}} - t$ years was modeled with an exponential function
 144 that decreases with constant mortality rate (d). Assuming constant mortality makes it easier to
 145 compare the proposed approach with the standard method (Hett and Loucks 1976).

146

147 **2.2. Simulated Data**

148 We used simulated age structures from tree populations in which mortality rates and the
 149 relationship with rainfall were known to assess the performance of HBA and the standard
 150 method in recovering these parameters. The estimates from both methods were compared with
 151 the “true values” to assess their power, including bias, precision, and coverage (Bolker 2008).
 152 Bias, the mean difference between the estimate and the parameter, was statistically assessed
 153 through a t test. The precision of the estimate was assessed through the confidence and credible
 154 interval widths, which are indicators of the uncertainty of the estimates. Coverage was
 155 calculated as the proportion of analyses in which the true parameter value is included within the
 156 estimated confidence or credible intervals.

157

158 Test data were generated by simulating rainfall, establishments and mortality over a period of
 159 1000 years, enough to deplete the oldest age classes under any of the considered mortality rates.
 160 For every year, rainfall was sampled from a normal distribution with mean 150 cm and standard
 161 deviation of 10 cm, which constitute an index of rainfall variability and were determined
 162 arbitrarily.

163

164 $R_t \sim \text{Normal}(150, 10)$ for $t = 1, \dots, T$

165

166 Establishments followed eq 1, where parameter b took values of -3, 3 and 10, and parameter a
167 was set to 1000. Surviving trees at age class c were simulated using eq 2, where d took the
168 values of 0.001, 0.005, 0.01 and 0.05 year⁻¹. Age structures were generated from a sample of
169 250 trees, which is within the limits of many dendrochronological age structure reconstructions
170 (e.g. Daniels and Veblen 2004). At least 100 age structures for every combination of parameters
171 b and d were simulated, but about 12% were discarded because the Markov Chains Monte
172 Carlo of the HBA failed to converge. The standard methods' estimates of the discarded analysis
173 were farther from parameters than the mean of the remaining estimates.

174

175 **2.3. Comparison between methods**

176 In the standard method a negative exponential curve is fitted to the age structure (Hett and
177 Loucks 1976). Point estimates of mortality (d) and their 95% confidence intervals were recorded
178 directly; but the estimates of the rainfall coefficients (b) and their 95% confidence intervals were
179 scaled to the whole population multiplying them by the ratio between sample and population
180 size.

181

182 We also used HBA that estimates all parameters simultaneously. The HBA model was
183 implemented in WinBUGS, a software designed to perform Bayesian inference via Markov
184 Chain Monte Carlo simulations (Spiegelhalter 2003). Flat, uninformative priors for all
185 parameters were used so that data dominated the results. For all parameters, three Markov chains
186 were started at random locations and updated 400.000 times; the convergence of the chains was
187 evaluated through the "potential scale reduction factor" $\hat{R}$ (Gelman and Rubin 1992). The joint
188 posterior distributions of the parameters resulted from combining the independent chains after

discarding the first 200,000 steps and keeping every third observation to reduce autocorrelation. The mean of the combined chains was used as point estimates for parameters and the 95% highest posterior density interval was used to estimate credible intervals. As with the standard method, the estimate of b and its credible interval were scaled to the whole population.

2.4. An example with Alder field data

We compared the standard and proposed approaches analyzing dendrochronological data sets from *A. acuminata* (Alder) forests from NW Argentina. Alder is a pioneer species distributed in mountain ranges from Mexico to NW Argentina. In northwestern Argentina the tree-line is dominated by this species, so it is expected that the establishment is controlled to some extent by climate (Holtmeier and Broll 2005). In xeric environments tree establishment might be enhanced in wet years (e.g. Daniels and Veblen 2004). In contrast, in environments with higher water availability temperature might be the main constraint to tree establishment; rainy periods are cloudy and cool, and thus, establishment could be associated with dryer (and warmer) years. For example, in montane systems of northwestern Argentina a negative association between rainfall and temperature has been observed. In this systems tree growth of different species is controlled by rainfall or temperature alternatively depending on the water availability of the site (Villalba et al. 1998). Accurately assessing the effect of rainfall on tree establishment would have implications in forest forecasting and management.

From 1997 to 2007 the age structures of Alder forests from ten watersheds of northwestern Argentina were constructed using dendrochronology (Fig. 2). The selected watersheds were characterized by a mosaic of patches covered by grasslands, shrublands, or Alder-dominated forests. In each watershed between 150 and 700 boles of *A. acuminata* were sampled with increment borers to date tree establishment. Grau and Veblen (2000) estimated that this species

grows at least 18 cm in the first year. Thus, to obtain the innermost ring, trees were cored within 18 cm of the soil from the downhill side of the tree to reduce problems in the manipulation of the borer handle. After counting backwards from the outermost to the innermost ring and correcting for non-attained centers (Duncan 1989) we reconstructed the age structures of the forests of each watershed.

219

Rainfall records are scarce in the study area and they are restricted to lowland areas, while *A. acuminata* dominates montane forests. In this exercise we used a single rainfall series from San Miguel de Tucumán (26°48'S, 65°12'W), one of the longest (it begins in 1884) and most reliable records in the region. Tree establishments occur during rainy springtime, from October to December and seedlings must harden before the beginning of the winter. We rescaled rainfall records between October of the establishment year (Y_0) and March of the following year (Y_1) to have a mean of zero and a standard deviation of one and used them as an indicator of the climate conditions. Although we acknowledge that temperature might affect the water balance of the environment, we consider that extrapolation from lowlands to highlands could increase the noise of the proxy. Analyses were restricted to the 20th century when more than 99% of the sampled trees were established.

231

232 3. Results

Under high simulated mortality ($d \geq 0.01$), both, the standard method and HBA recovered similar estimates (Fig. 1 a, b, e, f, i, j, Table S1). With low mortality ($d \leq 0.005$) the standard approach estimated d with some bias, even estimating negative mortalities when mortality was set to 0.001 (Fig. 1 c, d, g, h, k, l, 1, Table S1). The d estimates of HBA were always more precise than those of the standard method; the standard deviation of the mortality estimate obtained with the standard method was about twice of that obtained through HBA when $d \geq 0.01$ (Fig. 1 a, b, e,

f, i, j, Table S2). The difference increased to four times with low mortality ($d=0.005$, Fig. 1 c, g, k), and this difference was two orders of magnitude higher when parameter d was 0.001 (Fig. 1 d, h, l).

242

The 95% confidence intervals of the estimated mortality from the standard method and the 95% credible intervals of the HBA included the true d parameter value 92.5% and 95% of the time respectively, despite the fact that the confidence intervals of the first approach were wider than the credible intervals of the HBA (Tables S3, S4). Confidence intervals were two orders of magnitude broader than the corresponding credible intervals under very low mortality rates ($d=0.001$) and this difference decreased to between 3 and 1.3 times when mortality was higher ($d\geq 0.005$).

250

On average, the rainfall coefficient (b) was more precisely estimated by HBA than by the standard approach, implying that HBA estimated this coefficient with no bias in contrast with the standard method. The difference in the performance of both methods increased with the magnitude of the parameter and in general, the standard approach underestimated its magnitude (Fig. 1, a, b, e, f, i, j, Table S5). Bias in b estimates obtained with the standard approach was positively associated with mortality rates (Fig. 1, Table S6), being significant ($p<0.001$) whenever mortality was high ($d\geq 0.01$, appendix a). Under very low mortality rates ($d=0.001$) the standard approach estimated b almost as well as HBA, which correctly estimated it under all combinations of parameters.

260

The parameter for the effect of rainfall on tree establishment (b) was contained within the 95% confidence and credible intervals of estimates (coverage) 78% of the time with the standard approach and 93.5% of the time with HBA (Table S7). This coverage was above 90% with the

standard method when mortality was low or very low ($d \leq 0.005$), it decreased to around 85% under high mortality ($d=0.01$) and with very high mortality ($d=0.05$) coverage decreased again to just 48%. Meanwhile, the coverage of parameter b with HBA remained above 90% under all combinations of parameters. The width of the 95% credible intervals of the rainfall coefficient estimated through HBA was on average similar to the 95% confidence interval of the standard approach (Table S8). The analyses of coverage show that the standard approach overestimates the precision of b parameter, while HBA is more realistic.

271

The analysis of *A. acuminata* populations with both approaches produced different results. The mortality estimate was in general higher with HBA than with the standard approach. However, in Cerro Bravo the standard method estimated a high mortality, which was above 0.1, far from the rest of the populations that were between 0.001 and 0.04. Mortalities estimated with the proposed method ranged from 0.004 to 0.05 (Fig.3). In the five watersheds with highest mortality rates, the 95% credible interval of HBA and 95% confidence interval of standard method did not include the point estimate of the other method (Table S9).

279

Although both methods estimated negative rainfall coefficients b for six out of 10 sheds, some important differences were observed (Fig.3). None of the b estimates of the standard approach were significant since all the 95% confidence intervals included zero. In contrast, HBA identified two populations in which the 95% credible interval of the estimate was completely below zero. This method also identified a population (Volcán, one of the most xeric environments) with a positive b estimate that did not include zero in its 95% credible interval (Table S9).

287

288 4. Discussion

289 We used a simple model to highlight the advantages of modeling unobserved variables instead
290 of using a single surrogate of past events to estimate population parameters in historical ecology.
291 A simulation experiment showed that the estimates of mortality and rainfall coefficients of
292 forest dynamics attained through Hierarchical Bayesian Analysis (HBA) were more precise and
293 accurate than those obtained through the standard approach. Although in some scenarios the
294 average estimated mortality (d) was similar with both approaches, estimates were more accurate
295 with HBA under a broad set of combinations of parameters. This apparent contradiction is
296 explained by the high dispersion of d estimates among standard analyses in comparison with
297 HBA, suggesting that the former is unstable. Moreover, having similar coverage, the average
298 95% confidence interval of the standard method was broader than the corresponding interval of
299 the HBA showing that this estimate was more precise (Tables S3, S4).

300

301 Historical reconstructions are expensive; replicates are not always available, and usually
302 inferences are based on single data sets, so analyses should take full advantage of reliable
303 methods, especially when they are used to inform environmental policies. The estimation of
304 mortality in *A. acuminata* populations illustrates this point. In five out of 10 watersheds, neither
305 the 95% credible interval of HBA nor the 95% confidence interval of the standard method
306 included the point estimate of the other method (Table S9). The high dispersion of mortality
307 estimates obtained through the standard method in the simulation analysis (Fig. 1, Table S4)
308 suggests that HBA is more reliable. Thus, the high mortality rate estimated for Cerro Bravo by
309 the standard method could be an effect of this instability. Historic ecology has been proposed as
310 the best tool to depict environmental base-lines for landscape management (Egan and Howell
311 2001), so errors in the estimates of sensitive parameters such as mortality (Pinero et al. 1984)
312 could mislead the interpretation of the processes that shape landscapes. In contrast with the
313 standard method, which relies on a single estimate of mortality to infer past events progressively

314 compounding errors, HBA models the establishment process and mortality simultaneously. This
315 is useful to accurately characterize the age structure of the population and to take into account
316 different sources of uncertainty when estimating environmental effects on tree establishment,
317 which are overlooked by the standard approach. For example, in the standard method the rainfall
318 coefficient (b) is estimated given a point estimate of mortality (d), so all the uncertainty is
319 assigned to b . In the simulation experiment the b estimate of the standard method was biased
320 and its confidence intervals were inaccurate (Tables S5, S6). In contrast, HBA estimated
321 realistic, though wider credible intervals. Differences were also observed when empirical data
322 were analyzed; mortality estimates for the studied forests ranged between 0.001 and 0.1 with the
323 standard method and between 0.004 and 0.05 with the proposed method. The HBA detected
324 important effects of rainfall on alder tree establishments in 3 out of 10 watersheds, which were
325 deemed not significant by the standard approach. These differences may have implications in the
326 understanding and forecasting of forest dynamics.

327

328 Tree-lines shift in response to environmental change is a worldwide issue, whose mechanisms
329 have not been totally elucidated (Trant and Hermanutz 2014). Accelerating global changes will
330 continue to affect environmental patterns, so an accurate knowledge of the mechanisms that
331 control ecosystems will be critical to understand, predict and manage them. Climate warming
332 has been proposed as the main cause of tree-line advance (Harsch et al. 2009) but other causes
333 such as interaction with rainfall were also reported (Daniels and Veblen 2004; Wang et al.
334 2006). The HBA approach identified associations between rainfall and *A. acuminata*
335 establishments, which were undetected by the standard approach (Table S9). This is a plausible
336 association since tree establishment on grasslands depends on environmental constraints
337 (Sankaran et al. 2004). Differences in the sign of the associations could be explained by
338 variations in rainfall regimes; global warming pushes forests upwards only when water is

339 available (Holtmeier and Broll 2005). Rainy years are cooler, so in environments where water is
340 available a negative association between rainfall and establishment is expected. In contrast, in
341 more xeric environments establishment is mainly constrained by water availability. The
342 simulation experiment evidenced that the b estimate of the standard method was biased mainly
343 under high mortality rates ($d \geq 0.01$, Fig. 1, Table S6), which are within the ranges observed in
344 *A. acuminata* populations suggesting that estimated differences between both methods are not
345 spurious.

346

347 Although we used a simplified model to facilitate the comparison of the performance of both
348 methods we acknowledge that forest dynamics is not so simple. Aráoz and Grau (2010)
349 observed that, at the scale of stands, tree establishment was facilitated by fire events, which in
350 turn were controlled by climate. These complex interactions are beyond the scope of the present
351 study, which addresses forest dynamics at the watershed scale. However further studies
352 addressing these interactions at multiple scales are necessary to understand and forecast forest
353 dynamics. The HBA framework is specially designed to deal with complex problems in which
354 different hierarchical structures (e.g. in space or time), hidden variables, processes and their
355 uncertainties can be considered to estimate the parameters of the model (Clark 2005). Bayesian
356 methods provide adequate tools to combine different sources of information, which is useful in
357 historical ecology where information is scarce. One of the main advantages of Bayesian analysis
358 is the straightforward formulation of the models and the possibility of estimating unobservable
359 processes such as those involved in historical ecology (e.g. Boreux et al. 2009).

360

361 Here, tree populations were analyzed separately to compare the performance of both methods
362 but the empirical data could have been analyzed within a hierarchical framework, in which the
363 regional climatic effect could be separated from the local watershed effect. The implementation

of this framework would be straightforward by adding a watershed index and hyper-parameters under in the HBA, but it would be quite difficult in the standard approach (Gelman and Hill 2007). In this study we illustrated the use of HBA to infer tree population dynamics from dendrochronological data, but the logic of this approach could be applied to infer processes from data obtained through other techniques of historical ecology which are generally affected by loss of evidence or by other sources of uncertainty. For example, this approach could enhance reconstructions of disturbance regimes in which the evidence is erased by vegetation succession and by new disturbance events. HBA could also shed some light on palynological studies in which the contribution of each species to the record and its uncertainty could be modeled instead of using a single proxy.

374

We presented a Bayesian approach to model hard-to-get historic ecological data, which outperformed the current best available method in recovering known parameters. An empirical data set illustrated the power of HBA, which detected associations between rainfall and tree establishment in expanding subtropical montane forests which were not detected through the standard method. The use of latent variables to model unobserved processes in combination with an enhanced flexibility allowed by Bayesian analysis will constitute an essential tool to depict historic environments more accurately taking advantage of different sources of information.

382

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Figure captions

Fig. 1. Point estimates of the simulated tree population parameters. Point estimates of rainfall coefficient (b) and mortality rate (d) under the standard (black circles) and the proposed

approach (HBA, gray circles). Crosses represent the combination of parameters used in simulations.

Fig 2. Map of the position of the 10 watersheds analyzed. The cross indicates the position of the meteorological station of San Miguel de Tucuman. 1) El Centinela, 2) Taficillo, 3) Yala, 4) Volcán, 5) San Andrés, 6) La Quebradita, 7) Hualinchay, 8) Cerro Bravo, 9) Medina, 10) Tañ Sur.

Fig. 3. Point estimates of real tree population parameters. Point estimates of rainfall coefficient (b) and mortality rate (d) under the standard (black circles) and proposed approach (HBA, gray circles) for *Alnus acuminata* populations of ten watersheds from northwestern Argentina. 1) El Centinela, 2) Taficillo, 3) Yala, 4) Volcán, 5) San Andrés, 6) La Quebradita, 7) Hualinchay, 8) Cerro Bravo, 9) Medina, 10) Tañ Sur.

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1 **Supplementary material**

2 **Table S1. Average point estimate of mortality rate (*d*) under both approaches.**

True <i>d</i>	<i>d</i> =0.001		<i>d</i> =0.005		<i>d</i> =0.01		<i>d</i> =0.05	
True <i>b</i>	SM	HBA	SM	HBA	SM	HBA	SM	HBA
<i>b</i> =-3	-0.0075	0.0011	0.0046	0.0051	0.0098	0.0100	0.0497	0.0497
<i>b</i> =3	-0.0016	0.0011	0.0049	0.0050	0.0097	0.0098	0.0505	0.0495
<i>b</i> =10	0.0002	0.0010	0.0048	0.0050	0.0099	0.0099	0.0502	0.0494
Average	-0.0031	0.0011	0.0048	0.0050	0.0098	0.0099	0.0501	0.0495

3 Average point estimate of mortality rate is presented for every combination of true parameters
4 under standard method (SM) and under the proposed Hierarchical Bayesian Analysis (HBA). The last
5 row shows the average of all the simulations.

6 Table S2. Standard deviation of point estimate of mortality rate (d) under both approaches.

True d	$d=0.001$		$d=0.005$		$d=0.01$		$d=0.05$	
True b	SM	HBA	SM	HBA	SM	HBA	SM	HBA
$b=-3$	0.0384	0.0003	0.0018	0.0004	0.0014	0.0007	0.0045	0.0034
$b=3$	0.0507	0.0002	0.0013	0.0003	0.0013	0.0007	0.0053	0.0032
$b=10$	0.0426	0.0003	0.0013	0.0003	0.0017	0.0007	0.0054	0.0030
Average	0.0438	0.0003	0.0014	0.0004	0.0015	0.0007	0.0051	0.0032

7 Standard deviation of point estimate of mortality rate (d) for every combination of true parameters
8 under standard method (SM) and under Hierarchical Bayesian Analysis (HBA). The last row shows
9 the average of all the simulations.

10 **Table S3. Coverage of point estimate of mortality rate (*d*) within the 95% credible and confidence**
11 **intervals.**

True <i>d</i>	<i>d</i> =0.001		<i>d</i> =0.005		<i>d</i> =0.01		<i>d</i> =0.05	
True <i>b</i>	SM	HBA	SM	HBA	SM	HBA	SM	HBA
<i>b</i> =-3	0.98	0.94	0.94	0.92	0.92	0.93	0.92	0.97
<i>b</i> =3	0.97	0.97	0.89	0.96	0.94	0.93	0.89	0.96
<i>b</i> =10	0.96	0.96	0.94	0.95	0.92	0.94	0.92	0.98
Average	0.97	0.96	0.93	0.95	0.93	0.93	0.91	0.97

12 Coverage of point estimate of mortality rate (*d*) within the 95% credible and confidence intervals for
13 every combination of true parameters under standard method (SM) and under Hierarchical Bayesian
14 Analysis (HBA). The last row shows the average of all the simulations.

15 **Table S4. Average width of 95% confidence and credible intervals of point estimate of mortality**
 16 **rate (d).**

True d	$d=0.001$		$d=0.005$		$d=0.01$		$d=0.05$	
True b	SM	HBA	SM	HBA	SM	HBA	SM	HBA
$b=-3$	0.3058	0.0010	0.0048	0.0014	0.0051	0.0026	0.0171	0.0131
$b=3$	0.1276	0.0010	0.0043	0.0015	0.0052	0.0026	0.0168	0.0130
$b=10$	0.2948	0.0010	0.0044	0.0014	0.0052	0.0026	0.0168	0.0131
Average	0.2473	0.0010	0.0045	0.0014	0.0052	0.0026	0.0169	0.0131

17 Average width of 95% confidence and credible intervals of point estimate of mortality rate (d) for
 18 every combination of true parameters under standard method (SM) and under Hierarchical Bayesian
 19 Analysis (HBA). The last row shows the average of all the simulations.

20 **Table S5. Average point estimate of parameter *b* under both approaches.**

True d	<i>d</i> =0.001		<i>d</i> =0.005		<i>d</i> =0.01		<i>d</i> =0.05		<i>Average</i>	
True b	SM	HBA	SM	HBA	SM	HBA	SM	HBA	SM	HBA
<i>b</i>=-3	-1.55	-2.78	-2.64	-4.36	-1.08	-2.62	-0.65	-2.57	-1.32	-2.90
<i>b</i>=3	1.77	4.97	1.67	2.68	0.45	1.10	0.58	3.10	0.97	2.71
<i>b</i>=10	13.21	14.22	5.24	9.53	4.67	12.07	2.49	11.24	5.42	11.58

21 Average point estimate of parameter *b* for every combination of true under standard method (SM)
22 and under Hierarchical Bayesian Analysis (HBA). The last column shows the average of all the
23 simulations.

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24 **Table S6. Average bias of point estimate of parameter (b) for every combination of true**
 25 **parameters under both approaches.**

True d	<i>d=0.001</i>		<i>d=0.005</i>		<i>d=0.01</i>		<i>d=0.05</i>		<i>Average</i>	
True b	SM	HBA	SM	HBA	SM	HBA	SM	HBA	SM	HBA
<i>b=-3</i>	1.45	0.22	0.36	-1.35*	1.91***	0.38	2.35***	0.43	-1.68***	0.10
<i>b=3</i>	-1.22	1.97	-1.33	-0.31	-2.55***	-1.90*	-2.42***	0.10	-2.03	0.66
<i>b=10</i>	3.21	4.22	-4.76***	-0.47	-5.33***	-0.47	-7.51***	1.24	-4.57***	1.58

26 Average bias of point estimate of parameter (b) for every combination of true parameters under
 27 standard method (SM) and under Hierarchical Bayesian Analysis (HBA). The last column shows the
 28 average of all the simulations. *, **, *** indicates p value of t test below 0.05, 0.01 and 0.001
 29 respectively.

Table S7. Coverage of point estimate of scaled parameter *b* within the 95% credible and confidence intervals under both approaches.

True d	<i>d</i> =0.001		<i>d</i> =0.005		<i>d</i> =0.01		<i>d</i> =0.05		<i>Average</i>	
True b	SM	HBA	SM	HBA	SM	HBA	SM	HBA	SM	HBA
<i>b</i> =-3	0.92	0.92	0.98	0.96	0.80	0.90	0.22	0.94	0.70	0.92
<i>b</i> =3	0.93	0.93	0.98	0.96	0.92	0.92	0.77	0.95	0.90	0.94
<i>b</i> =10	0.96	0.94	0.94	0.94	0.87	0.94	0.46	0.93	0.75	0.94

Coverage of point estimate of scaled parameter *b* within the 95% credible and confidence intervals for every combination of true parameters under standard method (SM) and under Hierarchical Bayesian Analysis (HBA). The last column shows the average of all the simulations.

35 **Table S8. Average width of 95% confidence and credible intervals of point estimate of b parameter**
 36 **under both approaches**

True d	$d=0.001$		$d=0.005$		$d=0.01$		$d=0.05$		<i>Average</i>	
True b	SM	HBA	SM	HBA	SM	HBA	SM	HBA	SM	HBA
$b=-3$	61.14	20.75	9.53	13.70	7.46	17.34	3.34	13.48	20.19	16.66
$b=3$	131.37	57.91	27.95	42.43	16.67	37.12	8.48	34.94	41.37	41.97
$b=10$	248.71	88.82	41.60	61.17	28.52	63.43	14.56	61.25	62.71	66.36

37 Average width of 95% confidence and credible intervals of point estimate of b parameter for every
 38 combination of true parameters under standard method (SM) and under Hierarchical Bayesian
 39 Analysis (HBA). The last column shows the average of all the simulations.

40 **Table S9. Estimates of *Alnus acuminata* population parameters**

		Year		Standard approach						Hierarchical Bayesian Analyses						
							<i>b</i> estimate			<i>d</i> estimate			<i>b</i> estimate			
Sheds	N	I (19..)	F (19..)	<i>d</i>	95% CI		<i>b</i>	95% CI		<i>d</i>	95% CI		<i>b</i>	95% CI		
El Centinela	147	03	94	0.014	0.007	0.022	0.000	-	0.001	0.001	0.019	0.012	0.026	0.000	-	0.003
Taficillo	202	12	97	0.030	0.020	0.040	0.000	-	0.002	0.002	0.041	0.034	0.048	0.003	-	0.009
Yala	468	01	97	0.014	0.009	0.019	0.001	-	0.002	0.004	0.019	0.015	0.022	0.001	-	0.004
Volcán	267	01	99	0.019	0.011	0.027	0.001	-	0.001	0.004	0.016	0.011	0.021	0.003	0.001	0.006
San Andrés	269	07	99	0.001	-	0.009	0.002	-	0.004	0.001	0.004	0.000	0.008	0.002	-	0.004
La Quebradita	280	00	99	0.020	0.014	0.026	0.002	-	0.003	0.000	0.026	0.021	0.031	0.005	-	0.010
Hualinchay	296	01	99	0.004	-	0.009	0.000	-	0.002	0.002	0.006	0.001	0.010	0.000	-	0.002
Cerro Bravo	301	00	99	0.104	0.066	0.142	0.001	-	0.005	0.003	0.046	0.040	0.052	0.001	-	0.008
Medina	155	12	97	0.038	0.027	0.049	0.001	-	0.002	0.001	0.050	0.041	0.059	0.003	-	0.009
Tafí (sur)	718	01	99	0.030	0.024	0.037	0.002	-	0.006	0.003	0.040	0.037	0.044	0.012	-	0.022

41 Estimates of *Alnus acuminata* population parameters (mortality rates -*d*- and rainfall-tree
42 establishment relationship -*b*-) from ten watersheds from northwestern Argentina under the
43 standard and the proposed approaches. N: number of samples; I: initial year; F: final year.


```
44  Bug model
45  model{
46      for(i in 1:(nobs)){
47
48
49          N[i]~dpois(lambda[i])
50
51          lambda[i] <- max(a + b* rainfall1[i],0)
52
53
54
55          p[i] <- exp(-d * timelag1[i])
56
57
58          agestructure1[i] ~ dbin(p[i],N[i])
59
60      }
61
62      a~dnorm(0,0.0001)
63
64      b~dnorm(0,0.0001)
65
66      d~dunif(0,10)
67  }
```