Bustamante *et al.*
Revista Chilena de Historia Natural (2023) 96:6
https://doi.org/10.1186/s40693-023-00118-0

Revista Chilena de
Historia Natural

RESEARCH **Open Access**

On the use of *prior* distributions in bayesian inference applied to Ecology: an ecological example using binomial proportions in exotic plants, Central Chile

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Abstract

Background The use of Bayesian inference (BI) is a common methodology for data analysis in Ecology and Evolution. This statistical approach is particularly useful in cases which information is scarce, because allows formalizing sources of information, other than sampling data (*priors*), obtained from technical reports, expert opinions and beliefs. Recent reviews detected that most ecological studies use non-informative *priors* without any justification, ignoring other sources of independent information available to construct informative *priors*. In this study, we examined how the selection of informative or non-informative priors, affects hypothesis testing. We compared the proportion of occupied sites (occupancy) in four exotic plant species living in two contrasting environments in Central Chile. Given that occupancy is related to binomial proportions, we developed a statistical procedure based on beta distribution, to compare occupancies using Bayes factor.

Results Bayes factor obtained from different non-informative priors led to similar inferences relative to H_0. The use of informative prior drastically changed our decisions about H_0 in three of four plant species.

Conclusions The selection of priors is critical because they determine hypothesis testing. The use of independent information will improve our inferences, which is precisely the strength of BI. We hypothesize that the reluctance to use informative priors in ecological studies reflects extreme positivism and the use of non-informative priors is a strategy to avoid subjectivity; by doing that, ecologists depart from the philosophy of BI which accepts that the subjective knowledge is a valid, and sometimes the only alternative, to know the world.

Keywords Bayesian inference, Bayes factor, Binomial proportions, Prior distribution, Posterior distribution

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Background

Bayesian Inference (BI) is increasingly recognized as a useful statistical method in Ecology and Evolution [9, 16]. BI differs from Frequentist Inference (FI) because BI integrates sampling data with independent information obtained from other sources. BI is particularly appropriate for studies of Conservation Biology and Restoration Ecology because of data deficiencies that currently exist in endangered species and ecosystems [18]; in these cases, the use of statistical methods which considers other sources of information, is strongly recommended to anticipate proper conservation decisions [2].

Two kinds of functions are required to conduct BI: (i) the likelihood function which represent sampling data and (ii) a prior distribution which represent independent information. In BI, the parameters of interest are always random variables while and data condition their probabilities; in FI, parameters are fixed while data are random variable. If we multiply the likelihood function by the prior distribution, we can obtain the posterior distribution, i.e. $f(\theta|data)$, which represents an updated knowledge of the probabilistic properties of the parameters.

Another difference between BI and FI is the process of hypothesis testing. BI enables the calculation of the probability of different hypotheses H_i, given the available data, $P(H_i|data)$, in contrast to FI which evaluates the probability of data given the hypotheses $P(data|H_i)$ [9, 28]. BI calculates the probabilities to decide in favor or against hypotheses [17]. Using the Bayes Factor (BF), we can decide in favor or against a particular hypothesis. BI is conceptually supported by the Bayes theorem, which is the basis of conditional probability theory [20].

The use of independent information constitutes the foundation of BI [27]; prior distributions resume independent information and its investigation is a critical part of BI research [27]. Prior distributions can be classified as informative, when they reflect some knowledge about the parameters of interest, which properly analyzed, allows to obtain some estimations of the mean/median/mode as well as standard deviation of the parameters of interest [3]. On the other hand, non-informative priors represent situations in which we have no previous knowledge about the parameters of interest. Among a suite of non-informative prior distributions, the uniform distribution is one of the most utilized; this is an extreme case, where the absence of knowledge of the parameter of interest, gives equal probabilities to the whole range of the parameters [3, 15, 19].

A recent review about the use BI in Ecology reported that prior distributions are mostly utilized with no further justifications [3]. Even more, only 9% of studies published in five influential ecological journals between 2014 and 2018 ($n = 187$), used informative priors [19]. This situation is noteworthy because the process of hypothesis testing can change drastically depending on the selection of prior distributions [12]. The reasons to invoke the use of non-informative priors in Ecology is the absence of independent information. We sustain that independent information existing in technical reports as well as by experts opinion should be more utilized for the construction of informative priors [21].

One way to evaluate the impact of prior selection in BI is throughout sensitivity analysis. Basically, we can compare the impact of the use of different priors on the inference process [7]. The Bayes factor (BF) provides a tool to sensitivity analysis as it allows to compare results obtained from different priors [30]. Briefly, BF is the ratio of the probability of one hypothesis P(Ho|data) to the probability of another hypothesis P(H1|data). If BF is higher than 1, then evidence supports Ho; if BF is lower than 1, then evidence supports H1. BF constitutes a proper estimate to test whether different priors, impacts (or not) our decisions during hypothesis testing [19].

In this study, we aimed to compare BF contrasting informative vs. non-informative priors. Our hypothesis is that we expect different decisions in hypothesis testing if we use informative or non-informative priors. As an ecological example, we compared occupancy (i.e. the fraction of occupied sites in a region) in four exotic plant species living in two contrasting environments: Coast and Central valley, Central Chile. Given that occupancy is basically a binomial proportion [8, 29],we can use beta distribution to provide a methodology to construct the BF which allowed us to compare species occupancy between Coast and Central valley.

Methods

Conceptual background

Let us consider two vectors of independent random variables X_i and Y_j such that

$$\underline{X} = (X_1 \ldots, X_n),$$

$$\underline{Y} = (Y_1, \ldots, Y_m),$$

$$X_{1,} \ldots, X_n|\theta_1 \sim Bernoulli(\theta_1), \theta_1 \varepsilon [0, 1],$$

$$Y_{1,} \ldots, Y_m|\theta_2 \sim Bernoulli(\theta_2), \theta_2 \varepsilon [0, 1].$$

Let us define the joint vector of parameters $\underline{\theta} = (\theta_1, \theta_2) \varepsilon [0, 1]^2$. If $\underline{X}$ and $\underline{Y}$ are independent, then the likelihood function is given by.

$$L\left(\theta_1, \theta_2 | \underline{x}, \underline{y}\right) = \theta_1^{\sum_{i=1}^{n} x_i} \left(1 - \theta_1\right)^{n - \sum_{i=1}^{n} x_i} * \theta_2^{\sum_{j=1}^{m} y_j} (1 - \theta_2)^{m - \sum_{j=1}^{m} y_j}. \quad (1)$$

Under the assumption that θ_1 and θ_2 are independent, the prior bivariate distribution is the product:

$$\pi(\theta_1,\theta_2) = \pi(\theta_1) * \pi(\theta_2). \quad (2)$$

In our case, we assume that the prior marginal distributions of θ_k, with $k = 1,2$, are given by the beta distributions:

$$\pi(\theta_1) = \frac{\theta_1^{\alpha_1-1}(1-\theta_1)^{\beta_1-1}}{B(\alpha_1,\beta_1)},$$

$$\pi(\theta_2) = \frac{\theta_2^{\alpha_2-1}(1-\theta_2)^{\beta_2-1}}{B(\alpha_2,\beta_2)}.$$

These distributions represent informative beta priors because the hyperparameters can be elicited from other sources of information; for comparison, we can use non-informative priors which are conjugates of the beta distribution: Uniform (Beta 1,1), Jeffrey (Beta 0.5, 0.5) y Haldane (Beta 0,0).

The posterior bivariate distribution is given by the product of two univariate beta distributions:

$$\pi\left(\theta_1,\theta_2|\underline{x},\underline{y}\right) = Beta\left(\theta_1|a_1 = \sum_{i=1}^{n} x_i + \alpha_1,\ b_1 = n - \sum_{i=1}^{n} x_i + \beta_1\right)*Beta\left(\theta_2|a_2 = \sum_{j=1}^{m} y_j + \alpha_2, b_2 = m - \sum_{j=1}^{m} y_j + \beta_2\right), \quad (3)$$

where $Beta(\theta|a,b)$ is the univariate density function of a beta distribution with parameters a and b.

For the purposes of our study, we proposed the following statistical hypotheses:

$$H_0 : \theta_1 \leq \theta_2,$$

$$H_1 : \theta_1 > \theta_2.$$

Then the Bayes factor is defined as an *odds ratio*:

$$BF_{01} = \frac{\frac{\pi\left(H_0|\underline{x},\underline{y}\right)}{1-\pi\left(H_0|\underline{x},\underline{y}\right)}}{\frac{\pi(H_0)}{1-\pi(H_0)}}, \quad (4)$$

The posterior probability of H_0 is given by

$$\pi\left(H_0|\underline{x},\underline{y}\right) = \int_0^1 Beta(\theta_2|a_2,b_2)\left[\int_0^{\theta_2} Beta\left(\theta_1|a_1,b_1\right)d\theta_1\right]d\theta_2, \quad (5)$$

and the prior probability of H_0 is

$$\pi(H_0) = \int_0^1 Beta(\theta_2|\alpha_2,\beta_2)\left[\int_0^{\theta_2} Beta\left(\theta_1|\alpha_1,\beta_1\right)d\theta_1\right]d\theta_2. \quad (6)$$

Likelihood functions

We used presence/absence data of four exotic leguminous plants: *Acacia dealbata, Cytisus striatus, Teline monspessulana* and *Ulex europaeus.* These data were recorded from 30° to 43° south latitude, using two transects, one located along the Coast and the other, at the Central Valley. Within the transect, we disposed plots (2×50 m) placed along the verge of secondary or tertiary roads, with low management practices; each plot was located each 10 km encompassing a total of 264 plots (132 plots per transect). This information allowed us to estimate the occupancy of species at regional level either for Coast and Central Valley. For hypothesis testing, we compared occupancy between Coast versus Central Valley for each species. Our expectation was that exotic species should perform better at the Coast than at the Central Valley, given that at the Coast, the oceanic influence reduces temperature variation and increase air humidity relative to the Central Valley (the basic information gathered to construct the likelihood function is in Additional file 1: Appendix section).

To construct the informative priors**,** we used an independent study [10] which utilized a similar protocol to our field work. Shortly, they collected presence/absence data for the four species at the Coast and Central Valley in the Biobío and La Araucanía Regions, in south-central Chile, between 36° 35´ and 38° 25´ Lat S. They disposed 109 plots distributed along four of the principal highways which cross the study area. These plots were separated systematically approximately 5 km from each other. We distinguish plots of the Coast and Central Valley, simply using as separation line the coastal mountains: plots existing from the highest altitude toward the ocean were assigned as Coast while plots existing from the highest altitude to the east, were assigned as Central Valley.

Given the nature of the state variable (occupancy), informative priors are beta distributed (the basic information gathered to construct the informative prior distributions, is in Additional file 1: Appendix section). For the non-informative priors, we used three distributions: Uniform (Beta 1, 1), Jeffreys (Beta 0.5, 0.5), and an approximation of the Haldane distribution, (Beta 0.001, 0.001); here, it is clear that the Jeffrey's and Haldane's prior distributions are improper i.e. their integration between 0 to 1 is infinite. This fact constitutes one of the problems to the use of non-informative priors because in many cases they are not probability distribution functions [12]; working with improper priors can lead to the marginalization paradox [6] which means that the calculation of the Bayes factor can be affected by infinite value of the prior probabilities of H_0 and H_1. This is another argument to be cautious with the selection of priors. Even so, improper priors are still useful if posterior distribution are well defined [31].

To obtain posterior distributions, we simply multiplied the likelihood function by the specified priors, using Eq. (3) (see above). Finally, to obtain the Bayes factor BF_{01}, we applied Eqs. (4) to (6) (see above). By convention, data were presented as BF_{10} [17] which simply means that the numerator is $P(\theta|H_1)$ and the denominator is $P(\theta|H_0)$.

Results

In three species (*Acacia dealbata, Cytisus striatus* and *Teline monspessulana*) the posterior distributions constructed from informative priors were quite different to the posteriors constructed from non-informative priors (Figs. 1 and 2; Table 1). For instance, the mean values of the posteriors constructed from informative priors was more than 10% lower than the mean obtained from non-informative priors. The exception was *Ulex europaeus* in which posteriors distributions constructed from informative and non-informative these values were quite similar (Figs. 1 and 2; Table 1).

Using Bayes Factor, we changed our decision about the most plausible hypothesis, in three species. For instance, in *A. dealbata*, non-informative priors led us to decide in favor of H_0 while informative prior led us to decide moderately in favor of H_1 (Table 2); in *T. monspessulana* and *C. striatus* non-informative led us to decide in favor of H_1 but using the informative prior we decided strongly in favor of H_0 (Table 2); only in the case of *U. europaeus* both informative and non-informative priors led us to decide strongly in favor of H_1 (Table 2). Note that in this last species, although we maintained our decision about Ho, we observed a notable reduction in Bayes Factor using informative priors (criteria to decide in favor or against Hypothesis, were obtained from Andraszewicz et al. [1].

Discussion

We have shown that in three of four species, the change from non-informative to informative priors affected our interpretation of our results. The case of *U. europaeus* was the exception. This last situation is interesting because in this case, sampling data was sufficient to characterize posterior distribution and to conduct hypothesis testing. Our results, reinforce the idea to be cautious with the selection of priors in ecological studies.

If the selection of priors has been largely discussed in Bayesian Analysis as a potential source of confusion in hypothesis testing [27] why has it not received sufficient attention in Ecology? One possible explanation is the preeminence of positivism in Ecology and the false presumption that BI ought to be objective [23]. From positivism, data obtained from a well-designed sampling procedure, constitutes the only valid source of information; sources other than data, are not considered for statistical analysis [3]. Given that non-informative priors are well specified mathematical constructs, they supposedly add “objectivity” to the analysis, in opposition to informative priors which emerge from information gathered in other contexts, or are just are opinions and beliefs [3, 22, 26].

Subjectivity is present in any statistical approach either BI or FI [13]. However, in BI, subjectivity is explicitly recognized as part of the analysis and constitutes a strength rather than a weakness because it assumes that knowledge is always incomplete and preliminary [3, 14, 22]. We sustain that if an ecologist prefers non-informative over informative priors, he is refusing the use of a vast source of available information which exists outside peer-review journals and books (i.e. grey literature, [4]. As we said, this situation is particularly critical in Conservation and Restoration Biology [24]; in these disciplines, data are scarce and sometimes, the opinion of people (peasants, experts) constitute the only source of information; BI can assists the formalization of ecologically based informative priors using sophisticated techniques based on probability theory [5].

We strongly suggest that ecological studies use informative priors. BI is regarded as a continuous process that actualizes our knowledge about the parameters of interest in a virtuous circle of learning; for that reason, the knowledge is always preliminary [20]; if in the future we obtain new information, we can use the posterior distributions obtained for the first study, as an informative prior and thus conduct new BI that will update our knowledge about the parameters of interest. During this process, every piece of information is important, and BI provides a proper conceptual background for the integration of a variety of information. The only requirement is that selected priors must be clearly explicit about the rationale used for such selection.

In summary, prior distributions are a fundamental part of BI, either in its philosophy, interpretation, and model fitting; therefore, their selection should be considered carefully. We sustain that for ecologists, non-informative priors, can be mathematically adequate, but they do not account of the vast complexity of ecosystems. We encourage ecologists to initiate a debate about the use of informative priors when they are accessible [19]. As a guide to initiate this conversation, we suggest two ideas: (i) to consider grey literature [4, 25] and to learn about the elicitation process with experts or the public for the construction of informative priors [11] and (ii) to accept that subjectivity is part of BI, and

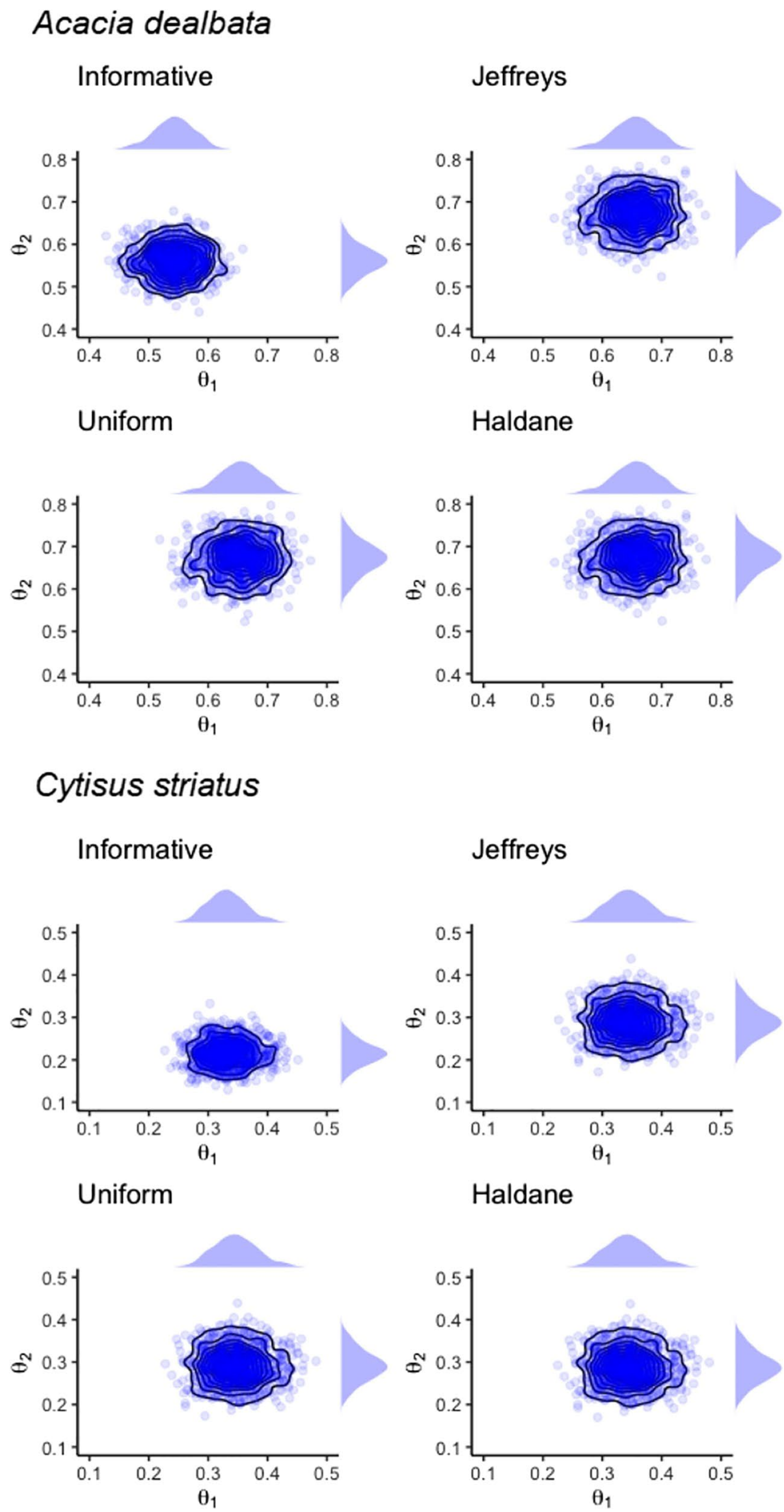

Fig. 1 Bivariate *posterior* distributions of two exotic species (*Acacia dealbata* and *Cytisus striatus*) obtained from one informative and three non-informative *priors*: Jeffreys, Uniform and Haldane. θ_1 represents the proportion of sites occupied at the Coast and θ_2 represents the proportion of sites occupied at the Central Valley. The univariate marginal posterior distributions are also depicted over each axe. The points in graphics resulted from a Monte Carlo simulation

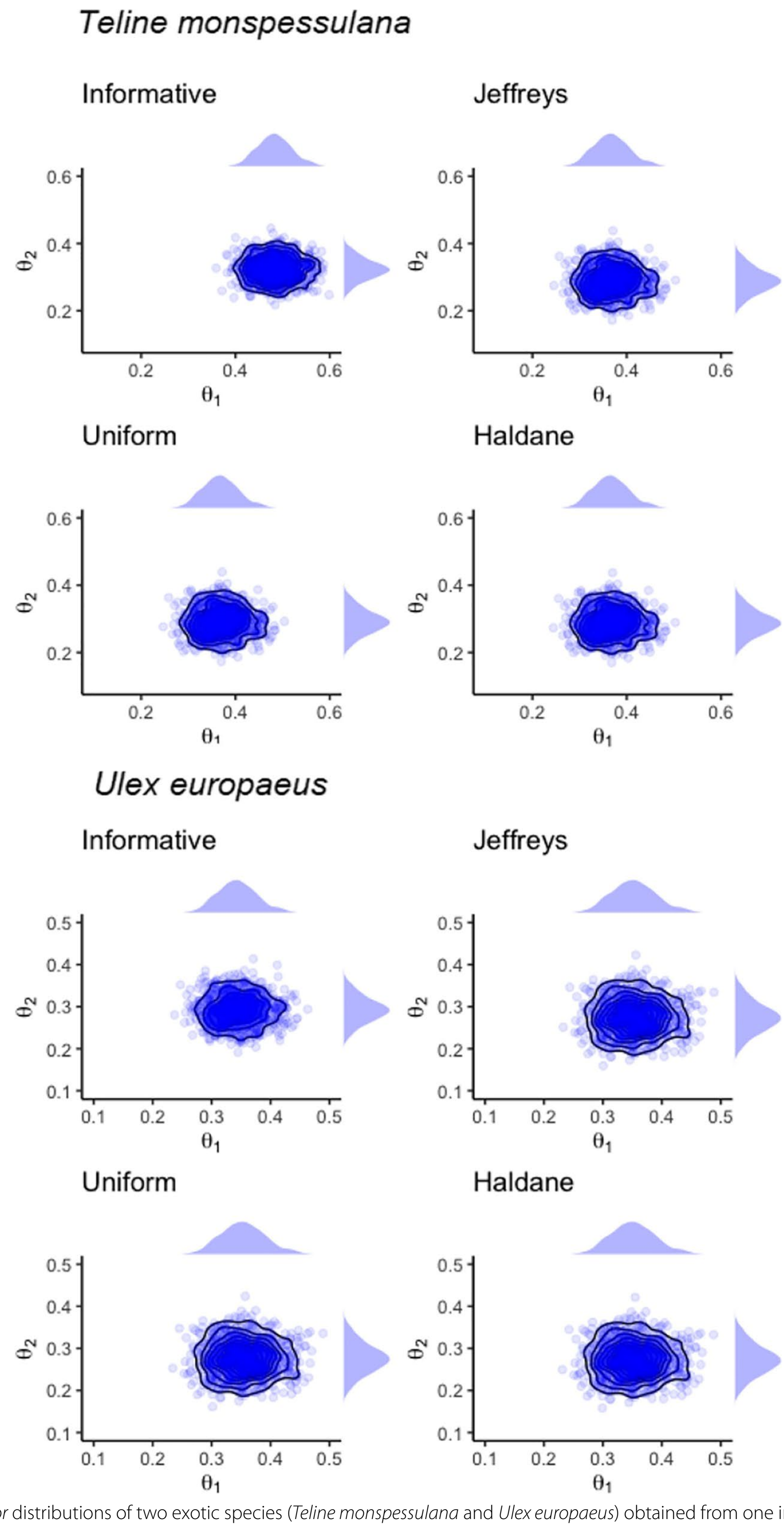

Fig. 2 Bivariate *posterior* distributions of two exotic species (*Teline monspessulana* and *Ulex europaeus*) obtained from one informative *prior* (obtained from independent information) and three non-informative priors: Jeffrey, Uniform and Haldane. θ_1 represents the proportion of sites occupied at the Coast while θ_2 represents the proportion of sites occupied at the Central Valley. The univariate marginal *posterior* distributions are also depicted over each axe. The points in graphics resulted from a Monte Carlo simulation

Table 1 Mean a standard deviation estimated from *posteriori* distributions obtained for four exotic plant species (*Acacia dealbata, Cytisus striatus, Teline monpessulana* and *Ulex europaeus*), using four a priori distribution (Informative, Jeffreys, Uniform and Haldane), Central Chile. θ_1 represents the occupancy of species in the Coast and θ_2 represents their occupancy in the Central Valley

Species	Informative	Jeffreys	Uniform	Haldane
Acacia dealbata	$\theta_1 : \mu = 0.5414$ $\sigma = 0.0369$ $\theta_2 : \mu = 0.6243$ $\sigma = 0.0359$	$\theta_1 : \mu = 0.653$ $\sigma = 0.041$ $\theta_2 : \mu = 0.675$ $\sigma = 0.04$	$\theta_1 : \mu = 0.6519$ $\sigma = 0.041$ $\theta_2 : \mu = 0.6741$ $\sigma = 0.040$	$\theta_1 : \mu = 0.6541$ $\sigma = 0.041$ $\theta_2 : \mu = 0.6761$ $\sigma = 0.0404$
Cytisis striatus	$\theta_1 : \mu = 0.333$ $\sigma = 0.0359$ $\theta_2 : \mu = 0.2143$ $\sigma = 0.0292$	$\theta_1 : \mu = 0.347$ $\sigma = 0.041$ $\theta_2 : \mu = 0.2873$ $\sigma = 0.0389$	$\theta_1 : \mu = 0.3481$ $\sigma = 0.0408$ $\theta_2 : \mu = 0.2889$ $\sigma = 0.0389$	$\theta_1 : \mu = 0.3459$ $\sigma = 0.041$ $\theta_2 : \mu = 0.2857$ $\sigma = 0.039$
Teline monspessulana	$\theta_1 : \mu = 0.4845$ $\sigma = 0.0393$ $\theta_2 : \mu = 0.3214$ $\sigma = 0.0333$	$\theta_1 : \mu = 0.35$ $\sigma = 0.0417$ $\theta_2 : \mu = 0.2873$ $\sigma = 0.039$	$\theta_1 : \mu = 0.3704$ $\sigma = 0.0414$ $\theta_2 : \mu = 0.2889$ $\sigma = 0.0389$	$\theta_1 : \mu = 0.3684$ $\sigma = 0.0417$ $\theta_2 : \mu = 0.2857$ $\sigma = 0.039$
Ulex europaeus	$\theta_1 : \mu = 0.345$ $\sigma = 0.0362$ $\theta_2 : \mu = 0.2908$ $\sigma = 0.0324$	$\theta_1 : \mu = 0.3545$ $\sigma = 0.0412$ $\theta_2 : \mu = 0.2724$ $\sigma = 0.0383$	$\theta_1 : \mu = 0.3556$ $\sigma = 0.041$ $\theta_2 : \mu = 0.2741$ $\sigma = 0.0382$	$\theta_1 : \mu = 0.3534$ $\sigma = 0.0413$ $\theta_2 : \mu = 0.2707$ $\sigma = 0.0384$

Table 2 Test for differences between occupancy estimates in the Coast (θ_1) and the Central valley (θ_2) in four alien plants, Central Chile, using Bayes Factor. Statistical hypotheses are $H_0 : \theta_1 \leq \theta_2$ and $H_1 : \theta_1 > \theta_2$. The Bayes factor was calculated using a) informative prior distributions (Beta distributions obtained from García et al. (2014); b) Uniform prior distributions, Beta (1,1); c) Jeffreys prior distributions, Beta (0.5,0.5), d) approximation to Haldane prior distribution, Beta (0.001,0.001). If Bayes Factor is higher than 1, then we support H_1; if values are lower than 1, then we support H_0.

Prior Distribution	*Acacia dealbata*	*Cytisus striatus*	*Teline monspessulana*	*Ulex europaeus*
Informative	4.970	0.186	0.028	8.994
Uniform	0.536	5.809	12.128	12.582
Jeffreys	0.534	12.302	12.302	12.767
Haldane	0.974	10.826	22.796	23.696

offers adequate procedures to formalize the uncertainty and our beliefs about the reality.

Conclusion

Bayesian inference conducted in ecological research use largely non-informative over informative prior distributions. In this study, we demonstrated that the selection of priors is crucial for hypothesis testing in Bayesian Inference. We compared occupancy in four exotic plants living in contrasting habitats in Central Chile. We found that our inferences changed depending on the kind of prior utilized, in the 75% of cases. We encouraged to ecologist to be very explicit during the selection of prior distribution. We also suggest that informative priors should be used more frequently in this kind of analysis.

Abbreviations

BI	Bayesian Inference
FI	Frequentist Inference
BF	Bayes Factor

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40693-023-00118-0.

Additional file 1.

Acknowledgements
To Marco Méndez and Alex Fajardo, who made critical comments to the final version of the manuscript.

Authors' contributions
ROB conceived the idea; AI and SF formalized it in statistical terms; RG contributed to the construction of the informative priors; Estefany Goncalves conducted the statistical analysis; all the authors contributed to the writing and edition of the manuscript.

Funding
Sandra Flores-Alvarado's Ph.D. studies are supported by ANID CONICYT-PFCHA/Doctorado Nacional/2020–21200398). RG and RO Bustamante were funded by Grant ANID/BASAL FB210006, RO Bustamante was funded by the Project Technological Center of Excellence CHIC-AND/BASAL PFB210018.

Availability of data and materials
Data utilized for this study are summarized in Appendix (see Supplementary materials).

Declarations

Ethics approval and consent to participate
Not aplicable.

Consent for publication
Not applicable.

Competing interests
The author(s) declare(s) that they have no competing interests.

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Received: 9 March 2023 Accepted: 20 June 2023
Published online: 01 August 2023

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