Decomposition of aquatic macrophytes: an inter-specific approach using model selection and multi-model inference

Decomposição de macrófitas aquáticas: uma abordagem inter-específica usando seleção de modelos e inferência multi-modelos

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Abstract: Aim: In this study, we used multiple statistical protocols to evaluate which nutrient content best explains senescent macrophyte and detritus decomposition of several macrophyte species in a lake of the Upper Paraná River floodplain; **Methods:** Senescent macrophytes of different life forms were left to decompose in litter bags. Macrophyte nutrient contents were quantified before and after incubation. Simple regressions, multiple regressions and Akaike information criterion were used to evaluate which nutrient best explained initial macrophyte decomposition and the decomposition of detritus that was partially decomposed. In addition, multi-model inference was used to generate models that explained decomposition rates; **Results:** The results showed that initial concentrations of phosphorus and carbon are the best predictors of decomposition rates of senescent tissues. When we evaluated the decomposition of partially decomposed detritus, the nitrogen content assumed an important role in determining decomposition rates. However, all candidate models had high explanatory strength; **Conclusions:** We argue that multi-model inference is a powerful strategy for explaining the impact of nutrient quality on macrophyte decomposition in the Upper Paraná River floodplain.

Keywords: macrophytes, decomposition rate, nutrient content, model selection, multi-model inference.

Resumo: Objetivo: Nesse estudo, utilizamos diferentes protocolos estatísticos para avaliar qual nutriente está mais relacionado com a decomposição de várias espécies de macrófitas senescentes e detritos em uma lagoa da planície de inundação do Alto Rio Paraná; **Métodos:** Tecidos senescentes de macrófitas pertencentes a vários tipos biológicos foram deixados para decompor em sacos de decomposição. A concentração de nutrientes foi quantificada antes e depois das incubações. Regressões simples, regressões múltiplas e o critério de informação de Akaike foram utilizados para avaliar qual nutriente está mais relacionado com a decomposição inicial das macrófitas e com a decomposição de detritos parcialmente decompostos. Adicionalmente, a inferência multi-modelo foi utilizada para gerar modelos para explicar os coeficientes de decomposição; **Resultados:** Os resultados mostraram que as concentrações iniciais de fósforo e carbono são os melhores nutrientes que explicam as taxas de decomposição de tecidos senescentes. Quando avaliamos a decomposição de detritos parcialmente decompostos, a quantidade de nitrogênio assume um importante papel na decomposição. Entretanto, nenhum dos modelos candidatos teve um alto poder de explicação; **Conclusões:** Concluímos que a inferência multi-modelo é uma estratégia poderosa para explicar a decomposição de macrófitas através da qualidade de nutrientes na planície de inundação do Alto Rio Paraná.

Palavras-chave: macrófitas, taxa de decomposição, quantidade de nutrientes, seleção de modelos, inferência multi-modelo.

1. Introduction

The decomposition of macrophytes is an essential process in aquatic ecosystems because it transforms organic matter and contributes to nutrient cycling (Wetzel, 2001; Rejmánková and Houdková, 2006). According to Meentemeyer (1984), at reduced spatial scales, factors such as the nutrient content of the detritus substantially affect decomposition rates. In fact, several authors highlight the effects of macrophyte detritus quality upon decomposition dynamics (Villar et al., 2001; Elger and Willby, 2003; Padial and Thomaz, 2006; Bragazza et al., 2007). It is widely accepted that higher amounts of nutrients such as nitrogen and phosphorus are associated with higher decomposition rates (Rejmánková and Sirová, 2007). Accordingly, predictive models of decomposition are based mainly on the chemical compounds of the plants (Bianchini Jr, 2003; Weerakkody and Parkinson, 2006).

Large data sets with decomposition rates from several different species are available (Bianchini Jr., 2003). However, studies reporting these data usually compare between species but do not look for trends across species. Additionally, most studies about macrophyte decomposition usually focus on only one or a few species (Pagioro and Thomaz, 1999; Villar et al., 2001; Padial and Thomaz, 2006). Macrophyte tissues of different life forms have widely different characteristics (Esteves, 1998), and such variety offers an excellent opportunity to analyze decomposition trends across species. Such variation makes it possible to apply, for example, a predictive approach; this approach has been used for several other limnological issues (maximum depth of macrophyte colonization predicted by Secchi disk, Chambers and Kalff, 1985, and maximum plant biomass predicted by littoral slope, Duarte and Kalff, 1986). In fact, predictive models also have the advantage of testing scientific concepts (Pace, 2001). For example, the generation of predictive models of decomposition is fundamental to making inferences about the main components associated with decomposition rates and to clarifying the dynamics of nutrients in ecosystems.

Two basic approaches have been used to interpret ecological data (Johnson and Omland, 2004). The first is based on null hypothesis tests, in which stepwise procedures are commonly used in multiple regression analyses. This approach has several recognized problems and pitfalls (Burnham and Anderson, 2002; Whittingham et al., 2006). For example, by maximizing the explanation coefficient (R^2) in traditional modeling, stepwise procedures always favor models with a high number of parameters and neglect the principle of parsimony (Johnson and Omland, 2004). By contrast, model selection offers an alternative way to draw inferences from a set of multiple competing hypotheses and takes parsimony into account (Burnham and Anderson, 2002).

Model selection is a robust framework that allows biologists to make inferences using modern statistical approaches (Johnson and Omland, 2004). In short, model selection can be understood by the selection of the best model (among a set of candidate models) using a criterion based on likelihood theory (usually Akaike information criterion or AIC, see Burnham and Anderson, 2002). This approach has its foundations in information theory and parsimony. Furthermore, studies with a predictive approach can use the so called multi-model inference commonly based on model averaging, an approach that uses information from all candidate models to estimate accurate coefficients (Burnham and Anderson, 2002).

In this study, we used macrophytes belonging to different life forms to look for decomposition trends across species. We aimed to evaluate which nutrient content best explains the decomposition of senescent macrophytes and detritus for several species in a lake of the Upper Paraná River floodplain. By using model selection, we first selected the best model among a set of candidate models that explain macrophyte decomposition rate through macrophyte chemical composition. Then, we used model averaging to make more precise correlations of macrophyte decomposition rates with macrophyte chemical composition.

2. Material and Methods

We selected 14 species of macrophytes belonging to different life forms that are common to the Paraná River floodplain (Brazil): *Chara guairensis* (R Bicudo), *Nitella furcata* (Roxburgh ex Bruzelius; C. Agardh emend R. D. Wood), *Cabomba furcata* (Schult & Schult.f), *Utricularia foliosa* (L.), *Egeria najas* (Planch.), *Potamogeton cf. pusillus* (L.), *Heteranthera* sp. (Ruiz & Pav.) (submersed); *Eichhornia crassipes* (Mart.; Solms), *Salvinia herzogii* (de la Sota) (free-floating); *Pontederia cordata* (L.), *Cyperus* sp. (L.), *Oxycaryum cubensis* (Poepp. & Kunth) (emergent); *Eichhornia azurea* (Kunth) (rooted with floating stems and emergent leaves); and *Nymphaea amazonum* (Mart. & Zucc.) (rooted with floating leaves). Senescent leaves and petioles of these species (ca. 100 g of fresh weight) were simultaneously left to decompose in litter bags (0.2 × 0.5 cm mesh) in the same lagoon of the Upper Paraná River floodplain. Therefore, limnological features (e.g., pH, oxygen, temperature) affected all bags similarly. To increase variation among samples, we also used only roots of *E. azurea* and *E. crassipes* in separate litter bags. We used three replicated litter bags per detritus type, resulting in 48 bags. Detritus dry mass was measured before and after 6 days of decomposition. Initial dry mass was measured by using extrapolations obtained for the independent relationships between fresh and dry mass for each species or each type of tissue used. The decomposition rates were estimated based on Olson's equation (Olson, 1963).

The concentrations of carbon (C), phosphorus (P) and nitrogen (N) in detritus were also quantified before and after incubation in the field (i.e., at day 6). After being weighed and pulverized, an aliquot (ca. 0.2 g) was combusted in a muffle furnace at 550 °C for 4 hours for the determination of carbon content relative to dry mass (after multiplying the remaining weight by 0.4; Allen et al., 1976). Phosphorus concentrations were measured in a spectrophotometer after acid digestion of an aliquot (0.3 g dry mass) and subsequent reaction with molybdenum using ascorbic acid (Mackereth et al., 1978). N concentrations were obtained after acid digestions of an aliquot (0.3 g dry mass) followed by steam distillation with a titrimetric finish (Kjeldahl nitrogen; Golterman et al., 1978).

We used two sets of predictors to explain decomposition rates: the nutrient contents of macrophytes measured before and after decomposition. This strategy was chosen because these two predictors represent different ecological meanings. By correlating initial nutrient contents with decomposition rates, we aim to explain the future decomposition of senescent macrophytes. Alternatively, by using nutrient contents after decomposition as predictors, we attempt to explain the decomposition of partially-decomposed detritus (after 6 days of decomposition in situ).

Firstly, we used simple regressions (linear or non linear) with C:N, C:P and N:P ratios (calculated both with nutrient contents measured before and after decomposition) as exploratory variables and decomposition rate as the response variable. Ratios were used because they are thought to be more strongly related to decomposition than the nutrient concentrations alone (Day, 1982). Secondly, we used multiple linear regressions based on standard stepwise procedures, with C, N and P concentrations as predictors. Again, we used both the nutrient contents before and after decomposition. For these analyses, we considered significant relationships when the type I error was less than 0.01.

In addition to these traditional techniques, we used model selection based on Akaike information criterion corrected for small samples (AICc) to select the model that best explains the decomposition rate from among a set of candidate models. The lowest AICc value indicates the best model (Burnham and Anderson, 2002). Similarly to the simple and multiple regressions, we used two sets of predictors to generate two sets of candidate models. The first set was comprised of models that used C, P and N concentrations measured before decomposition as predictors. The second set used the nutrient contents after decomposition as predictors (i.e., at day 6). Each set of candidate models contained seven models; each model represented a linear relationship between one or more predictors and decomposition rate (e.g., model 1: just P as predictor, model 2: P and N as predictors, model 3: C and N as predictors, etc.). We chose this approach because the AICc value is a result of a parsimonious choice that maximizes the goodness-of-fit and minimizes model complexity (i.e., the number of predictors). Therefore, model selection can show different results compared to traditional techniques. Models were also compared by the Akaike weight (AICc wi); which is a measure of the relative likelihood of the model given the data. The AICc wis are normalized across the set of candidate models to sum one, and are interpreted as probabilities (Johnson and Omland, 2004).

Multi-model inferences based on model averaging were used for both sets of candidate models to enhance the accuracy in coefficient estimations. This is a procedure that gathers information of multi-models to produce a new and powerful model. It accounts for uncertainty in model selection in order to obtain robust estimates of model coefficients (Johnson and Omland, 2004). In this analysis, a constant and the coefficients of each variable are calculated, together with their standard error (Burnham and Anderson, 2002). Additionally, the generated coefficients are accompanied by an importance value based on the AICc wi (Johnson and Omland, 2004). This value indicates the relative importance of each predictor for the model generated by model averaging. SAM software (Rangel et al., 2006) was used for model selection procedures and multi-model inferences. STATISTICA software (Statsoft, 2005) was used for regressions analyses and to make figures.

3. Results

Decomposition rates varied from 0.0025 to 0.30 d^{-1} across species. Accordingly, macrophyte nutrient contents before (C: 20.48 to 38.14% Dry Mass; P: 0.03 to 0.28 $mg.g^{-1}$; and N: 0.47 to 2.50 $mg.g^{-1}$) and after decomposition (C: 15.67 to 39.32% Dry Mass; P: 0.04 to 0.61 $mg.g^{-1}$; and N: 0.53 to 7.54 $mg.g^{-1}$) also had wide ranges.

Only the simple regression using the N:P ratio before decomposition as a predictor of decomposition rate was not significant (Figure 1; it is important to note that if we have considered significant values when $P < 0.05$, simple regression using N:P would be significant). The other ratios (C:N and C:P) had significant ($P < 0.01$) non linear relationships with decomposition rate (Figure 1). In this case, simple regression with the C:P ratio as the predictor had the highest explanation coefficient ($R^2 = 0.43$; Figure 1). Multiple linear regression also revealed that only initial P and C concentrations were significant, with an adjusted coefficient of explanation of 0.405 ($k = 0.32 + 0.35*P - 0.44*C$; $P < 0.01$).

The best model, according to AICc criterion, correlates initial P and C concentrations with decomposition rates (Table 1). The goodness-of-fit of the best model is very similar to that of the second-best model (uses all nutrient contents as predictors). In spite of this, the best model has a reasonably higher AICc wi than the second-best model (Table 1). This is due to the parsimonious nature of model

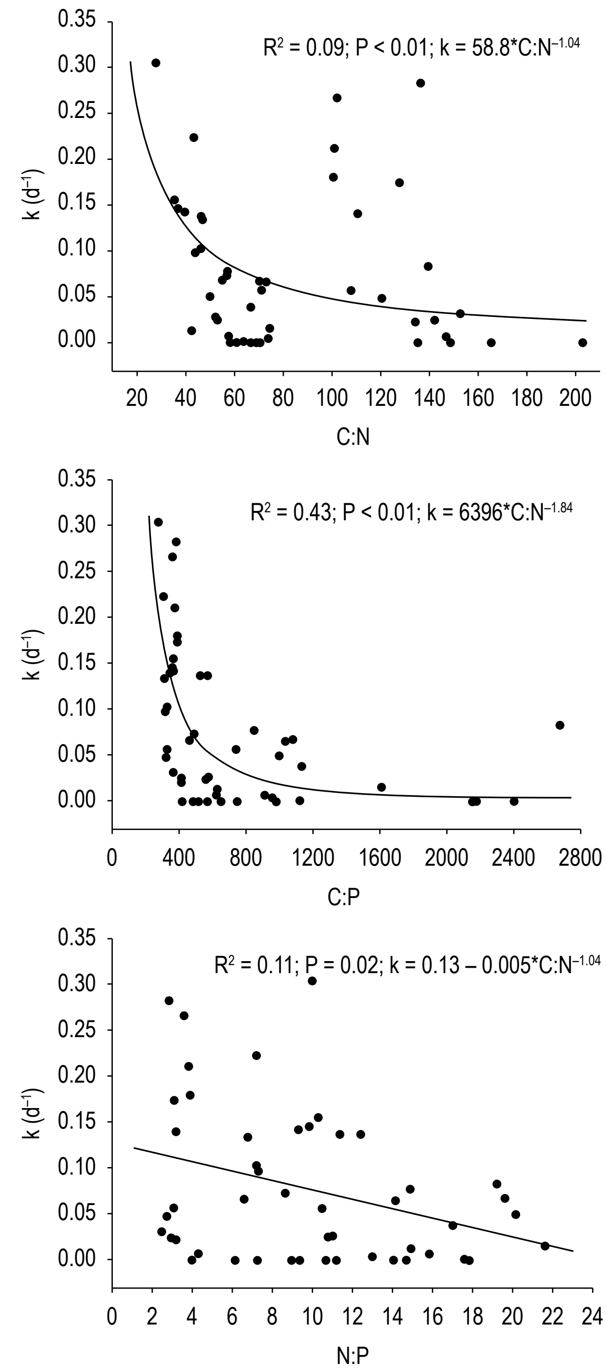

Figure 1. Simple regressions between decomposition rates and initial nutrient ratios. Equations are shown within the graphs. The explanation coefficient (R^2) and the significance of each model (P) are also shown. k = decomposition rate; C = Carbon; N = Nitrogen and; P = Phosphorus.

selection, which punishes models with more predictors. The coefficients of the model based on model averaging, together with their standard errors, are summarized in Table 2. The importance values also indicate that tissue P and C are the most important predictors of decomposition.

After six days of decomposition, simple regressions show that decomposition rates were significantly ($P < 0.01$) explained by the C:N and C:P ratios, using non linear equations (Figure 2; here again, if we have considered significant values when $P < 0.05$, simple regression using N:P would be significant). In addition, the C:N ratio was the best predictor of the decomposition rate of partially decomposed detritus according to the explanation coefficient ($R^2 = 0.40$; Figure 2). However, only N and P concentrations were significant predictors according to multiple linear regression ($R^2 = 0.66$; $k = 0.32 + 0.52*P – 0.47*N$; $P < 0.01$).

Table 1. Model selection procedure sorted by AICc for models correlating nutrient content (measured before decomposition) and decomposition rates. Adj R^2 means the adjusted coefficient of determination of the linear regression of each model.

Variables	Adj R^2	AICc	AICc wi
P, C	0.405	–120.407	0.692
P, N, C	0.400	–118.509	0.268
C	0.294	–113.481	0.022
N, C	0.299	–112.508	0.013
P	0.243	–110.165	0.004
P, N	0.234	–108.268	0.002
N	0.030	–98.264	<0.001

Table 2. Multi-model inference procedure showing the coefficients, with their importance values and their standard error, of each variable of the model based on multi-model inference (for models correlating nutrient content before decomposition and decomposition rate).

Variables	Importance	Coefficient	Standard error
Constant	-	0.329	0.102
P	0.965	0.445	0.141
N	0.283	0.014	0.005
C	0.994	–0.004	0.001

Similarly to the simple regressions, model selection elected the model that correlates C and N concentrations after decomposition with decomposition rates as the best among the candidate models, (Table 3). Coefficients based on model averaging, together with their standard errors, are shown in table 4. After decomposition, the importance values were similar among the three predictors (Table 4).

4. Discussion

The chemical composition of the selected macrophytes varied greatly and, thus, our samples from species belonging to different life forms represented a broad array of detritus nutrient contents and decomposition rates. This provides robustness to our models that explain decomposition rates across species through macrophyte chemical composition.

According to all the analyses that considered nutrient content prior to decomposition, P and C were the most important nutrients affecting these decomposition rates. The importance of these nutrients in decomposition has

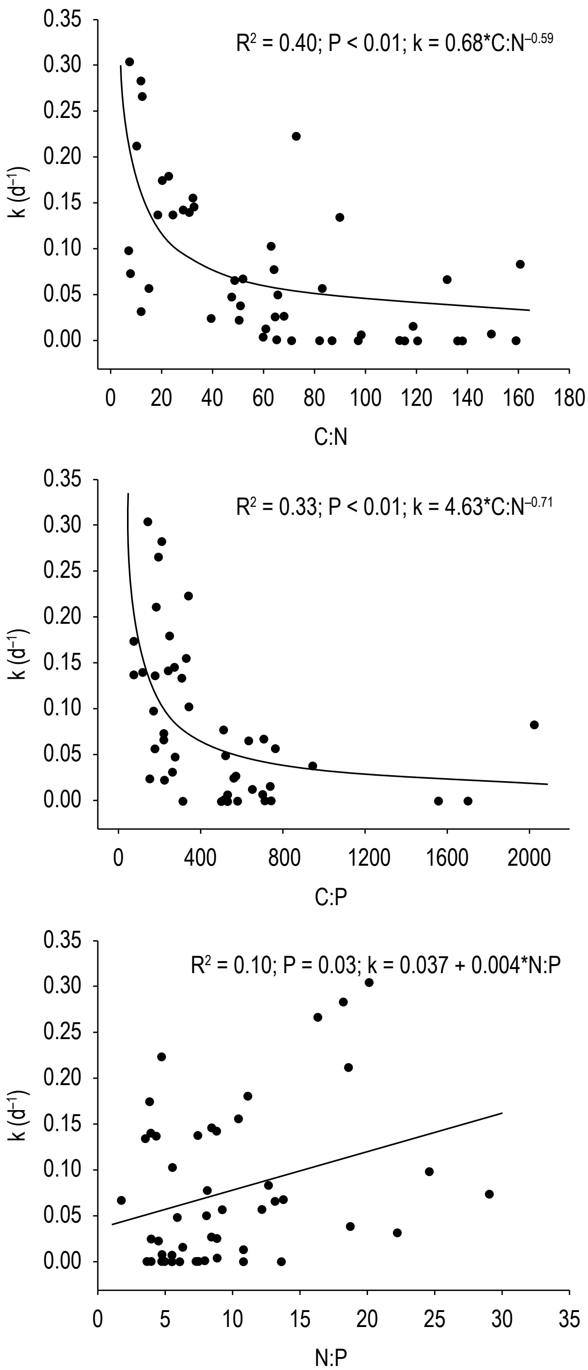

Figure 2. Simple regressions between decomposition rates and nutrient ratios of partially decomposed detritus. Equations are shown within the graphs. The explanation coefficient (R^2) and the significance of each model (P) are also shown. k = decomposition rate; C = Carbon; N = Nitrogen and; P = Phosphorus.

been found by others (Rejmánková and Houdková, 2006), and it is not a surprise in the Upper Paraná River habitats, where phosphorus has been considered the main limiting nutrient of microbial activity (Thomaz et al., 2001; Thomaz et al., 2004). Detritus richer in P is more susceptible to higher bacterial activities that lead to higher decomposition

Table 3. Model selection procedure sorted by AICc for models correlating nutrient content (measured six days of decomposition) and decomposition rates. Adj R^2 means the adjusted coefficient of determination of the linear regression of each model.

Variables	Adj R^2	AICc	AICc wi
N, C	0.376	–118.113	0.250
P, N, C	0.394	–118.077	0.246
P, N	0.375	–117.997	0.236
P	0.338	–116.625	0.119
P, C	0.356	–116.559	0.115
N	0.299	–113.841	0.030
C	0.236	–109.698	0.004

Table 4. Multi-model inference procedure showing the coefficients with their importance values and their standard error, of each variable of the model based on multi-model inference (for models correlating nutrient content after decomposition and decomposition rate).

Variables	Importance	Coefficient	Standard error
Constant	-	0.140	0.122
P	0.601	0.174	0.059
N	0.762	0.016	0.006
C	0.730	–0.002	<0.001

rates and faster dry mass losses. In addition, organic matter content (directly related to carbon content) is considered to be among the most important determinants of aquatic macrophyte detritus quality (Elger and Willby, 2003).

With our strategy of using multi-model inference (based on model averaging), we were able to generate a model relating decomposition rate to the initial chemical composition of macrophytes in the Upper Paraná River floodplain. According to Johnson and Omland (2004), model averaging should be used when the underlying goal of model selection is coefficient estimation or prediction and no single model is highly supported by the data (i.e., AICc wi for the best model < 0.9). Given that AICc wi of the best model was only 0.692 (Table 1), and explanation coefficients (R^2) were not conspicuously high, the use of this procedure seems reasonable to explain variability in macrophyte decomposition rates due to differences in initial nutrient contents. In model averaging, coefficients were calculated taking into account the relative importance of each nutrient; thus, representing a better attempt at explaining and maybe predicting macrophyte decomposition in this Neotropical floodplain.

After six days of decomposition, conflicting results were obtained by different analytical methods. The C and N concentrations of detritus are considered the important predictors according to AICc and simple regression models, but N and P concentrations are the most important predictors according to multiple linear regression. In addition, if only the goodness-of-fit is considered in model selection (instead of AICc), we would elect the model comprised by

C, N and P as the best one (Table 3). This would not be a parsimonious decision, however, given that the addition of P in the best model only slightly increases the goodness-of-fit (Table 3).

The probable reason for these conflicting conclusions is the fact that Akaike weights (AICc wis) were very similar among the first 5 models (Table 3). This indicates that the best model is not far better than the other following four and, if we take nutrient concentrations of detritus already decomposing into account, multiple causes may be limiting detritus decay. In fact, according to model averaging, the three nutrients were similarly important for explaining the decomposition of detritus that is already decomposing. This highlights the relevance of using multi-model procedures to make conclusions about which variables best explain decomposition rates of detritus.

The importance of nitrogen when using data of partially decomposed detritus is probably associated with the fact that nitrogen concentrations usually increase during decomposition (Esteves, 1998; Villar et al., 2001; Padial and Thomaz, 2006). This indicates that initial detritus nitrogen is not sufficient for decomposers, and most of the nitrogen comes from the water column. Thus, this can explain the fact that initial nitrogen is not a good predictor of decomposition. Given that nitrogen is immobilized in detritus during decomposition, this nutrient must be more related to decomposition rates of partially decomposed detritus.

There has been great discussion about the misuses and pitfalls of null hypothesis tests (Lukacs et al., 2007; Stephens et al., 2007). Thus, a new approach based on information theory and parsimony has been receiving great attention among ecologists. However, publications concerning model selection in ecology are mainly theoretical, and few studies use this approach in practical research or as a tool for testing multiple hypotheses. The current study presents an example of the use of this innovative approach to select models that aim to explain ecological processes (e.g., decomposition). Traditionally, we would use stepwise multiple regression, which is highly biased and has many shortcomings (Whittingham et al., 2006). Biases in coefficient estimation, inconsistencies among model selection algorithms and problems with multiple hypotheses testing are some drawbacks of stepwise multiple regression (Whittingham et al., 2006). Furthermore, model selection is appropriate for testing multiple hypotheses and is more powerful for solving inconsistencies when selecting the best model. This study provided us an opportunity to identify which nutrient is mostly related to macrophyte decomposition rates (an example of testing multiple hypotheses).

Nevertheless, this approach is not free of shortcomings. For example, model selection and multiple linear regressions draw distinct conclusions regarding the relationship between nutrient contents and decomposition rates of partially-decomposed detritus (see Results). Choosing one conclusion as correct is difficult and arbitrary. In spite of this, model selection offered us the opportunity to evaluate, through AICc wi, if the best model is good enough to draw conclusions or if multi-model inference should be used to mitigate biases.

In our case, since the two best models were not highly supported by the data (i.e., AICc wi < 0.9), they were not good enough to draw conclusions; therefore, multi-model inference should be used (Burnham and Anderson, 2002). In addition, linear regressions (both simple and multiple) also did not have conspicuously high explanation coefficients (R^2 always lower than 0.66). Multi-model inference clarified that all nutrients have similar importance to explain decomposition rates of partially-decomposed detritus. In addition, this approach can circumvent shortfalls of multiple regressions when the goal is to furnish predictive models (Whittingham et al., 2006). In this sense, we stress that multi-model inference, a still underused approach, seems to be a more reliable way to understand the decomposition of macrophytes.

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