ORIGINAL ARTICLE

Exploring the predictive performance of several temperature measurements on Neotropical dung beetle assemblages: Methodological implications

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Abstract

Basic characteristics of species assemblages are frequently related to temperature variables recorded at a coarse-grained scale. In this study, 15 min instant-measurements of environmental and soil temperatures were recorded during 1 year in six Atlantic Forest sites of southern Brazil, ranging from 250 to 1,630 m a.s.l. These measurements were used to examine the comparative explanatory capacity of several temperature variables in predicting species richness and total or specific variations of dung beetle abundance. The results suggest that temperature measurements obtained during the survey period have the highest explanatory capacity. Furthermore, average temperature values seem to have a relatively higher explanatory capacity than absolute minimum or maximum values reflecting extreme conditions. In general, there is no rule in selecting a temperature variable when the objective involves explaining the variation in species abundances. Both soil and air variables can have similar explanatory capacities. The present results should be considered when designing future ecological studies in Neotropical conditions.

Key words: Scarabaeinae, soil and air temperature, temperature explanatory capacity.

INTRODUCTION

Resources and conditions jointly drive the distribution of species. Resources are all things consumed or used by organisms (e.g. space, nutrients, water, prey and mates), and conditions are environmental factors varying in space and time and affecting the performance of an organism. Among environmental conditions, temperature has been traditionally considered as one of the most relevant abiotic factors in explaining biological phenomena (Chapman 1928; Huey & Kingsolver 1989) due to its influence on chemical and metabolic reactions (Gillooly *et al.* 2001). Consequently, the variation in the basic characteristics of species assemblages, as well as the occurrence and abundance of living organisms, has been frequently related with temperature variables (Begon *et al.* 2006), especially in the case of heterothermic animals, such as insects (Schowalter 2011). However, local temperature values are often sourced from the records of neighboring climatological stations or from maps that use these data to generate interpolated values at higher resolutions. Thus, local temperature data are frequently derived from averaging long periods and distant places, which ignore the microenvironmental and temporal variations in temperature truly experienced by the organisms (Dobrowski 2011; Pincebourde *et al.* 2016; Sheldon & Dillon 2016). Even when local temperature measurements are obtained by direct measurements, the most appropriate temperature measurement to use is sometimes unclear. Some questions may arise: Which variables are the most adequate to describe fauna variations – mean values representing average conditions or maximum/minimum values reflecting threshold temperatures? Are temperature records taken in air or soil the most suitable when the life cycle is closely linked to edaphic conditions? Should we use

previously recorded temperatures or those recorded at the same time as the survey?

Relationships between temperature conditions and the structure of dung beetle assemblages or the occurrence/abundance of certain species have been widely studied in different regions of the world (e.g. Landin 1961; Davis 1995; Sowig 1997; Zamora *et al.* 2007; Davis *et al.* 2008a,b; Agoglitta *et al.* 2012). However, very few studies analyze the predictive performance of temperature variables collected *in situ*, which reflect microenvironmental conditions (see Caveney *et al.* 1995; Krell *et al.* 2003; Krell-Westerwalbesloh *et al.* 2004; Davis *et al.* 2013). In this study, 15 min instant-measurements of environmental and soil temperatures were recorded continuously during 1 year in six Atlantic Forest sites in southern Brazil, ranging from 250 to 1,630 m a.s.l. These data are used to examine the comparative explanatory capacity of several temperature variables in predicting species richness and total or specific variations of dung beetle abundance, measured as the number of active species and individuals collected in each sampling unit. Although a high number of different and correlated variables can account for richness and abundance variations (altitude, forest type, productivity, soil type or resource availability), the aim here is specifically to explore the explanatory capacity of several temperature variables, which in turn are associated with other factors representing the change in the overall environmental conditions. Thus, the specific aims of this study are to explore whether: (i) a temperature variable has a comparative superiority in explaining both synecological and autecological variables; (ii) mean temperature values should be prioritized with respect to maximum or minimum values; (iii) soil temperature values are as effective as air measurements; and (iv) past recorded temperatures have a similar explanatory capacity as those estimated at the time of the survey. The obtained results could be considered to design future ecological studies.

MATERIALS AND METHODS

Study area

This study was carried out at six sites ranged from 250 to 1,630 m a.s.l. and comprising an altitudinal transect extending northeast to southwest (27°44′ to 28°9′S; 48°48′ to 49°37′W) in two Atlantic Forest formations in Santa Catarina state, southern Brazil (see da Silva *et al.* 2018 for further details): lowland Dense Ombrophilous Forest and upland Mixed Ombrophilous Forest.

In Santa Catarina, Dense Ombrophilous Forests occur from a few meters above sea level to approximately 800 m (IBGE 1992), being an evergreen forest whose canopy reaches 50 m, with emergent trees up to 40 m in height. It has dense shrub vegetation, consisting of ferns, bromeliads and palms. Creepers, epiphytes (bromeliads and orchids), cacti and ferns are also abundant. In humid soil, fig trees and palms, such as *Euterpe edulis* von Martius., are frequent. Its main feature is the ombrophilous environment related to the high rainfall in the coastal region of Brazil (up to 3,000 mm/year). In this forest, latosols and podzolic soils are predominant, with low fertility.

The Mixed Ombrophilous Forest is an ecosystem with rain throughout the year, occurring usually at high altitudes (between 800 and 1,700 m a.s.l.), and contains species of angiosperms and conifers. In southern Brazil, it occurs on the slopes of diabase hills mixed with sandstone metamorphosed by Cretaceous volcanism, which forms the Serra Geral mountainous formation. The Mixed Ombrophilous Forest is characterized by the presence of *Araucaria angustifolia* (Bertoloni) Kuntze, a very frequent Coniferae in this biome (IBGE 1992). In general, the climate in these Atlantic Forest formations of southern Brazil is subtropical, with regular rainfall and relatively well-defined seasons: winter is usually cold, with frequent frosts and snow due to the altitudinal influence. Temperatures range from below zero in winter to 30°C in the summer (IBGE 1992).

Sampling protocol

Dung beetles were sampled by using baited pitfall traps once a month between June 2015 and June 2016 (13 sampling periods). Pitfall traps comprised plastic containers (15 cm diameter × 20 cm depth) buried with the top edge at ground level. A small plastic dish, supported by wooden sticks, was placed approximately 10 cm above each trap to protect against rain. A mixture of water and neutral detergent (300 mL) was added to each container to retain trapped beetles. Human feces and rotting pork flesh (aged in plastic containers at room temperature 3 days prior to sampling) were used as bait (ca. 10 g of each) to attract dung beetles. Separately, each type of bait was wrapped in thin cloth and tied to the central part of the rain protection lid above the traps (da Silva & Hernández 2014, 2015a).

During each sampling period, each of the six sites was sampled using ten baited pitfall traps, distributed in pairs (10 m distant) along a transect. Each pair was spaced 100 m apart (da Silva & Hernández 2015b), and contained both types of baits separately. Data from

both types of traps were pooled and the complete inventory of every ten pitfall traps was considered a sampling unit. Samplings were undertaken for 48 h every month. We were not able to sample a few sites three times due to road obstruction (flooding): July 2015 for a site at 1,300 m; September 2015 and March 2016 for a site at 1,000 m. In total, there were 75 sampling units (= 13 sampling periods × 6 sampling sites − 3). Previous completeness analyses indicated that approximately 88% of the estimated total number of species present was collected at each site (da Silva *et al.* 2018).

Sampled beetles were sorted and identified using dichotomous keys (Vaz-de-Mello *et al.* 2011) and the expert taxonomical guidance provided by Dr. Fernando Vaz-de-Mello (Universidade Federal de Mato Grosso), who corroborated all identifications. Voucher specimens (dried and mounted onto entomological pins) were deposited in institutional collections (Universidade Federal de Santa Catarina, Florianópolis, and Universidade Federal de Mato Grosso, Cuiabá, Brazil). Most beetles were preserved in 90% alcohol. The permission to collect dung beetles was issued by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/MMA, permit # 49486-1), the Brazilian biodiversity regulatory institution. The complete list of the dung beetle species collected in each period and site with their respective abundances can be found at da Silva *et al.* (2018).

Origin of temperature variables

We measured air and soil temperature at each of the six sites using two waterproof data loggers (HOBO 64K Pendant; Onset Computer Corporation, Bourne, MA, USA). One data logger was placed 1 m above the ground and tied horizontally to a tree to measure environmental temperature, and the second was buried in the ground (5 cm) to measure soil temperature. Data loggers were installed at each site in the middle of each transect near the traps. Each data logger was programmed to take temperature measurements every 15 min throughout the sampling period. Moreover, data loggers were installed 11 days before the first dung beetle sampling. In parallel with these temperature measurements mean luminosity (ML) was also obtained with the same data loggers registering environmental air temperature. Additionally, a pluviometer was installed in an open area near each sampling site taking rainfall measurements during the 48 h of sampling (R) as well as the rainfall for an entire month before each survey (R_M).

From the raw temperature data, we calculated daily average, maximum, minimum and range of temperature for soil and air. Afterwards, we calculated 12 temperature measurements (°C) for each 48 h sampling period (i.e. measurements for sampling days only), for both air (A) and soil (S), as follows: mean temperature (MAT and MST), mean maximum temperature (MMAT and MMST), mean minimum temperature (MmAT and MmST), absolute maximum temperature (AMAT and AMST), absolute minimum temperature (AmAT and AmST) and temperature range (average temperature range during the 48 h sampling period; TAR and TSR). Additionally, average temperatures for the 2, 5, 7 and 10 days before each sampling period were also calculated for both air and soil (MAT2, MAT5, MAT7 and MAT10 and MST2, MST5, MST7 and MST10, respectively). Thus, the explanatory capacity of 23 climatic variables (20 of them related to temperature) was examined reflecting soil and air conditions during the survey as well during previous days.

Statistical analyses

General Linear Models (GLM) were used to estimate the individual explanatory capacity by using the classic coefficient of determination (R^2) of each of the considered temperature variables on species richness, total abundance in log (n + 1) and abundance variation of the 11 most characteristic dung beetle species (also in log (n + 1)). These species were selected as those appearing in more than 30% of total surveyed samples (n = 75) and/or more than 5% of total abundance. GLM with type III sum of squares were also used to estimate the partial effects of each type of temperature variable. Partial effects represent the "pure" variability accounted for by each temperature variable independently of all the other predictors included in the model (Legendre & Legendre 2012). Thus, the "pure" variability of each temperature variable was estimated: (i) when included together with just three other climatic variables (ML, R and R_M) (R^2_{TEMP}); or (ii) when all the other climatic variables are considered as covariates at the same time (R^2_{PURE}). Thus, a measurement of the individual explanatory capacity of each temperature variable was obtained, as well as measurements on their capacity to exclusively account for the variability in the response variables when other climatic predictors are included. The explanatory capacity in partial regressions was calculated as the ratio (in %) between the sum of squares of each variable and the total sum of squares. Finally, saturated models, including all the formerly mentioned predictors, were also carried out in order to estimate the complete variability accounted for

by the complete set of climatic predictors (R^2_{SAT}). The main purpose of these analyses is to estimate the individual explanatory capacity of the different temperature variables. Thus, correction of alpha values in multiple testing, multicollinearity and statistical significance are not a concern. All the statistics were calculated using Statistica 12.0 (StatSoft Inc. 2013).

RESULTS

Richness and abundance

The explanatory capacity of all temperature variables when considered together (R^2_{SAT}) is high: 74.85% for species richness and 70.53% for total abundance. For species richness, individual $R^2 \times 100$ values for each temperature variable exceeded 40%, except in the case of temperature range variables (TAR and TSR; see Table 1). Both air and soil temperature variables taken during the survey had the highest explanatory capacity,

particularly average conditions (MST and MAT $\approx$ 60%) and mean minimum temperatures (MmST and MmAT $\approx$ 58–59%). Both species richness and abundance increased with temperature, linearly and exponentially, respectively (Fig. 1).

Variables characterizing temperature conditions in the days prior to the sampling period were less relevant ($\approx$ 46%). In the case of total abundance, all the considered variables equaled or exceeded an explanatory percentage of 35%, except for temperature range (Table 1). MAT is the only variable surpassing 50%. Furthermore, some mean, maximum and minimum variables representing air and soil temperatures during the survey had a relatively high explanatory capacity (MMST, MmAT and MST; Table 1). Temperature variables characterizing temperature conditions in the days prior to the sampling period were, once again, less relevant ($\approx$ 34%).

When controlled by the effects of other types of climatic variables (rainfall and luminosity), the explanatory capacity of temperature variables (R^2_{TEMP};

Table 1 Individual explanatory capacity (measured by the coefficient of determination, R^2) of the considered climatic variables on the variation in dung beetle species richness and total abundance when each one is considered separately (R^2), as well as explained variability (R^2_{TEMP}) when other non-temperature variables are included as covariates (rainfall and luminosity), and "pure" variability of each when all climatic variables are considered together in a partial GLM (R^2_{PURE})

Species richness				Total abundance			
Variable	R^2	R^2_{TEMP}	R^2_{PURE}	Variable	R^2	R^2_{TEMP}	R^2_{PURE}
MST	60.37	43.25	0.74	MAT	51.49	27.87	1.05
MAT	60.13	43.46	0.57	MMST	46.83	27.16	0.01
MmST	59.34	40.47	0.14	MmAT	46.21	21.49	0.01
MmAT	57.77	41.62	0.11	MST	45.67	24.33	0.89
AmST	56.85	38.51	0.54	MmST	43.71	21.10	1.91
MMST	56.63	41.27	1.95	AMAT	43.30	18.83	0.50
AmAT	52.52	37.57	0.81	AmAT	42.31	19.61	0.01
MST5	49.18	36.68	0.29	AmST	42.27	20.90	0.09
MST7	48.40	36.93	0.00	AMST	42.15	23.47	2.21
MMAT	47.82	36.01	0.66	MMAT	40.96	24.98	0.00
AMST	47.77	34.35	2.10	MAT5	36.45	24.33	0.20
MST10	47.76	36.91	0.09	MAT10	35.89	25.87	1.27
MST2	47.09	35.36	0.01	MAT7	35.18	24.17	1.30
MAT5	46.08	33.15	0.01	MST10	34.52	24.18	1.81
MAT7	45.13	33.26	0.01	MST5	34.51	22.76	1.16
MAT10	44.58	33.50	0.00	MST7	33.87	22.88	1.59
AMAT	44.19	25.29	2.04	MAT2	32.93	23.82	0.37
MAT2	41.62	31.62	0.43	MST2	32.20	22.31	0.00
R_M	19.41	–	0.14	R_M	26.98	–	0.52
TSR	0.49	0.11	0.16	R	0.68	–	0.21
R	0.22	–	3.26	ML	0.06	–	4.28
ML	0.14	–	1.61	TSR	0.02	1.04	2.69
TAR	0.04	1.82	0.10	TAR	0.01	3.26	0.87

R^2_{TEMP} and R^2_{PURE} were calculated as the ratio between the sum of squares of each variable and the total sum of squares.
AmAT, absolute minimum air temperature; AMAT, absolute maximum air temperature; AmST, absolute minimum soil temperature; AMST, absolute maximum soil temperature; MAT, mean air temperature; ML, mean luminosity; MmAT, mean minimum air temperature; MMAT, mean maximum air temperature; MmST, mean minimum soil temperature; MMST, mean maximum soil temperature; MST, mean soil temperature; R, rainfall during the sampling period; R_M, rainfall during the entire month period before each survey; TAR, temperature air range; TSR, temperature soil range. MAT2, MAT5, MAT7, MAT10, MST2, MST5, MST7, MST10 are average temperatures for the 2, 5, 7 and 10 days, respectively, before each sampling period for air (MAT) and soil (MST).
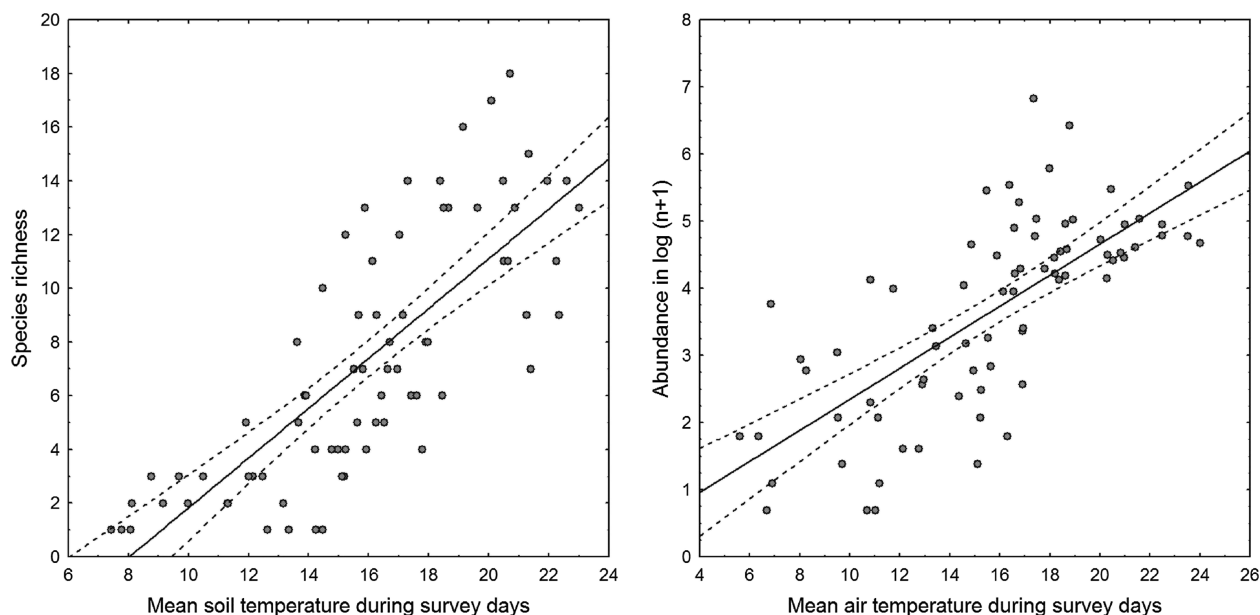
Figure 1 Instant measurements of environmental and soil temperatures were recorded during 1 year in six Atlantic Forest sites of southern Brazil to compare the explanatory capacity of several temperature variables in predicting species richness and variations of dung beetle abundance. The relationship between the mean soil temperature experienced during the survey days and species richness, and the mean air temperature experienced during the survey days and total abundance values in log (n + 1) were obtained in each sample unit (n = 75). The continuous line represents the linear regression of both values and the broken lines the confidence intervals at 95%.

Table 1) on species richness decreased by approximately 14% on average, but the most relevant variables remained constant (except in the case of MMST). The explained variability was $36.6 \pm 2.2\%$ (mean ± 95% confidence interval) if temperature range variables (TAR and TSR) are excluded (Table 1). In the case of abundance, the explanatory variability of temperature variables decreased by 17% on average, illustrating the limited effect of non-temperature climatic variables on abundance variations. In this case, the explanatory capacity of the different temperature variables is equal (from 18.8% to 27.9%; mean = $23.3 \pm 12.2\%$).

The "pure" explanatory capacity of temperature variables when all the other climatic variables are considered as covariates (R^2_{PURE}) is almost negligible (Table 1). Only some, mainly non-temperature variables, have exceeded the 2% barrier.

Species abundance variations

Saturated models including all the considered climatic variables account for important proportions of total variability in abundance variations of the different species (from 40% to 66%; Table 2). Interestingly, when the variables with a higher explanatory capacity are considered individually, those related to soil temperatures seem to be especially relevant. For 9 of the

11 species, soil variables, such as MST or MmST, explain the highest variability. In some cases, there are large differences in the explanatory capacity of the saturated models and those provided by individual temperature variables (Table 2; see *Canthidium* aff. *lucidum*, *Canthon angularis obenbergeri*, *Homocopris* sp. and *Uroxys* sp. 1), which indicates the importance of the combined effects of temperature variables in explaining abundance variations.

When the effects of rainfall and luminosity were included (R^2_{TEMP}), the individual explanatory capacity of temperature variables is only maintained relatively high for *Canthon rutilans cyanescens* (Harold, 1868) and *Dichotomius sericeus* (Harold, 1967) (Table 2) for MmST and AmST (see Fig. 2), respectively. In this case, variables representing minimum temperature values, such as MmST and MmAT, seem to be especially relevant. The "pure" explanatory capacity of temperature variables when all of climatic variables are considered as covariates (R^2_{PURE}) barely reaches 6% (Table 2), except in the cases of *Homocopris* sp. and *Uroxys* sp. 1 for MMAT and ML, respectively.

DISCUSSION

Temperature variables seem to be especially relevant to explain species richness variations in dung beetle

Table 2 Collected abundance and number of occurrence samples for each dung beetle species appearing in more than 30% of total surveyed samples (n = 75) and/or more than 5% of total abundance

	Canthidium aff. lucidum	Canthidium aff. trinodosum	Canthon angularis obenbergeri	Canthon rutilans cyanescens	Coprophanaeus saphirinus	Deltochilum brasiliense	Deltochilum morbillosum	Dichotomius sericeus	Homocopris sp.	Phanaeus splendidulus	Uroxys sp. 1
Abundance	274	657	845	636	225	163	212	467	228	155	1855
Occurrence	29	41	26	22	29	44	23	25	38	29	18
R^2_{SAT}	40.60	65.20	50.45	53.81	62.78	52.11	58.22	66.50	60.47	51.64	39.90
R^2	MmST	MmST	TSR	MST	MST	MMST	MST	AmST	MST	MmAT	ML
	(5.21)	(38.13)	(3.24)	(41.48)	(41.46)	(31.78)	(27.83)	(50.48)	(14.38)	(28.5)	(4.86)
R^2_{TEMP}	MmST	MmST	TSR	MmST	MST	MMST	MmAT	AmST	MmST	MmAT	MmAT
	(1.59)	(23.50)	(4.53)	(38.24)	(22.53)	(19.11)	(17.21)	(43.34)	(10.84)	(25.27)	(3.16)
R^2_{PURE}	MMAT	ML	MAT	TSR	R	ML	R	R	MMAT	MmAT	ML
	(4.09)	(6.79)	(6.11)	(3.56)	(4.44)	(4.54)	(3.67)	(2.92)	(12.67)	(2.75)	(14.23)

Explanatory capacity accounted for a complete saturated GLM (R^2_{SAT}) including all the considered climatic variables (in %) on the abundance variations of each species in log (n + 1), climatic variables with the highest individual explanatory capacity (R^2), temperature variables with the highest "pure" explanatory capacity (R^2_{TEMP}) when luminosity and rainfall are used as covariates (Type III sums of squares) and climatic variables with the highest "pure" explained variability (R^2_{PURE}) when all the other climatic variables are considered as covariates. R^2_{TEMP} and R^2_{PURE} were calculated as the ratio between the sum of squares of each variable and the sum of squares total. AmST, absolute minimum soil temperature; MAT, mean air temperature; ML, mean luminosity; MmAT, mean minimum air temperature; MmST, mean minimum soil temperature; MMAT, mean maximum air temperature; MMST, mean maximum soil temperature; MST, mean soil temperature; R, rainfall during the sampling period; TSR, temperature soil range.
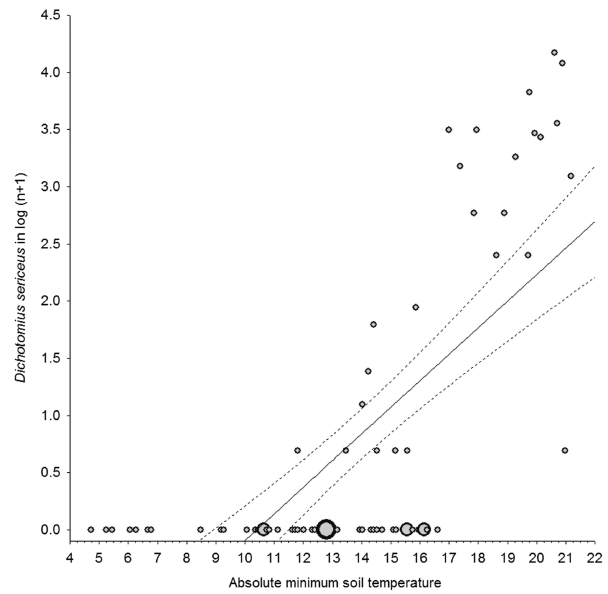

Figure 2 Relationship between the abundance variation in sampling units of *Dichotomius sericeus* and the absolute minimum soil temperature of each sampling period during 1 year in six Atlantic Forest sites of southern Brazil. The dot size is proportional to the number of observations with the same value.

assemblages. However, in general (Sagarin *et al.* 2006), abundance variability is more difficult to predict, even when a more diverse set of climatic variables is included. However, the obtained results suggest four basic recommendations in the case of adult dung beetles: (i) temperature measurements obtained during the survey period are the ones that have the highest explanatory capacity; (ii) average temperature values seem to have a relatively higher explanatory capacity than absolute minimum or maximum values, which reflect extreme conditions; (iii) there is no general rule in selecting a temperature variable when the objective involves explaining the variation in species abundances; and (iv) both soil and air variables can have a similar explanatory capacity.

There is a big difference between the complete explanatory capacity of the considered temperature variables together and the variability of each variable separately. This is a consequence of the high collinearity between the considered temperature variables, as well as the importance of their combined effects in explaining richness or abundance variations (i.e. the response variable cannot be accounted for by a single temperature variable). Despite collinearity between the different temperature measurements, taking temperature measurements directly during the survey period seems to guarantee more precise estimations about the role of temperature variables in explaining richness and

abundance variations of dung beetles, at least for the studied environmental conditions.

The practical implication of this result is that temperature measurements should be taken at the same time as assemblage or species abundance estimations, avoiding the use of interpolated values not directly related with the conditions experienced by the animals (Caveney *et al.* 1995; Krell *et al.* 2003; Krell-Westerwalbesloh *et al.* 2004; Davis *et al.* 2013). The general lack of relevance of temperature measurements when obtained in the days before the survey period also suggests a quick response from dung beetles to the modified climatic conditions. A close link between dung beetle activity and environmental temperature conditions might be an advantage in a group that must imperatively consume an ephemeral resource and attain a high body temperature for flight or to manage dung (Bartholomew & Heinrich 1978). Thus, special care must be taken in directly comparing different dung beetle assemblages when they experience different climatic conditions. The use of several local abundance and richness values obtained under a diverse set of climatic conditions can be viewed as an option to surpass this inconvenience.

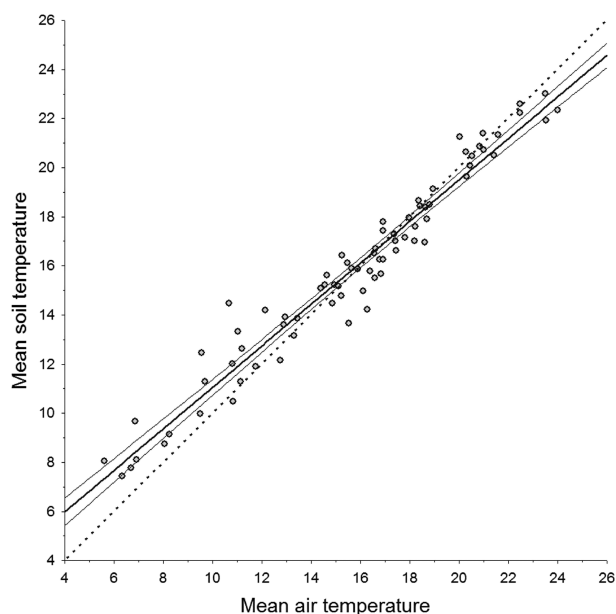Temperature variables representing average conditions during the survey period seem to have a higher explanatory capacity in the case of synecological variables than those reflecting extreme unsuitable temperature conditions. However, absolute minimum temperature might appear as relevant in accounting for abundance variations for some species (e.g. *Dichotomius sericeus*; Fig. 2). In fact, the most interesting result obtained here is that it is not possible to choose a unique temperature variable that is able to explain the variation in species abundances. Although variables representing soil and minimum temperature conditions seem to be particularly relevant, the truth is that the temperature with the highest explanatory capacity appears to be idiosyncratic and probably depends on the ecological and biological characteristics of each species.

Interestingly, soil temperature variables are equally or more important than air variables in explaining the variation in species abundances, possibly because these variables act as an "on/off switch" to indicate the existence of suitable climatic conditions outside. Soil temperatures hardly oscillate in forest biomes (Davies-Colley *et al.* 2000; Pincebourde *et al.* 2016) and the temperature buffering capacity of soil is higher than that of the air (Fig. 3), being fundamental in explaining the activity of some dung beetle species (Houston & McIntyre 1985; Krell *et al.* 2003; Krell-Westerwalbesloh *et al.* 2004). Considering that soil data loggers are harder to detect and steal, the acquisition and use of soil temperatures might be a promising and effective alternative to better understand the daily and seasonal activity of dung beetles.

ACKNOWLEDGMENTS

Figure 3 Linear relationship between air and soil temperatures (thick continuous line) $\pm$ 95% confidence intervals (thin continuous lines) during 1 year in six Atlantic Forest sites of southern Brazil. The broken line is the equality line. Note that soil temperatures are comparatively higher than air temperatures under cold conditions, but comparatively lower in hot conditions.

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