1 Investigating termite nest
2 thermodynamics using a quick-look
3 method and the heat equation

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17 Abstract

18 **Termite mounds are often cited as an example of efficient thermoregulated structures.**

19 **Nest thermal stability can be critical for insects that are particularly sensitive to heat and**

20 **desiccation. Few studies have measured internal temperature of termite nests with**

21 **respect to environmental parameters, especially in Neotropical species. In this study, we**

22 **analyzed the thermal profiles of different parts of *Procornitermes araujoi* nests, a**

23 **neotropical mound-building termite of the Brazilian *cerrado*. To read into our dataset we**

24 **first used rasterization, a method that allows a quick-look assessment of time-series. Our**

25 **results show that nest architecture efficiently buffers against environmental temperature**

26 **fluctuations while at the same time maintaining a relatively high internal temperature in**

27 **the core. This rather stable internal climate follows nevertheless the external temperature**

28 **long-term averages. Using a novel numerical scheme, we further show that the heat**

29 **transfer dynamics are well described by the classical heat equation, with an additional**

30 **heat source whose origin is discussed.**

Introduction

Nests are supposed to protect animals from hostile environmental conditions [1]. In social insects, nests can be considered as microclimate regulation devices (for gas exchange, temperature or humidity) and have intrigued researchers for decades [2–6]. They are also an inspiring source for human engineering applications [7–10]. Nest thermoregulation can be characterized as either active or passive [4]. Active thermoregulation is defined as mastered by insect behavior such as fanning behavior in bees [4] or the creation of an energy sink by bringing up underground water in termites [11]. On the other hand, passive thermoregulation relies on mechanisms such as nest site selection [4,12] or nest architecture [6]. An outstanding example of passive thermoregulation is the ventilation system developed by some ant and termite species to increase the ventilation of their underground chambers [7,13–17].

Nest temperature is highly influenced by external periodic forcing. Even if the nest structure generally permits a good regulation of the internal microclimate, nest temperatures often follow short term (daily) and long term (weekly, annual) environmental fluctuations [7,18]. In mound-building species, like the African termite *Trinervitermes sp.,* the temperature fluctuations are more important in the upper part of the mound than inside the core [18,19]. Here, we investigate temperature dynamics in the Neotropical termite *Procornitermes araujoi* Emerson (1952) [20]. This species is endemic to the Brazilian *cerrado* (savanna). Its colonies inhabit nests that are characterized by medium-sized mounds usually rising less than 1m above ground (**Fig 1a**). The internal architecture is relatively simple with an homogeneous foam-like structure (**Fig 1a**) [21,22] also found in *Trinervitermes sp* or even in ant species like the black-garden ant *Lasius niger* [23]. It lacks the complex ventilation systems found in fungus-growing termites [15,24] or in leaf-cutting ants [14]. It is thus a convenient species to study nest thermoregulation in simple architectures with lower metabolic activity compared to fungus growing species.

Fig 1. Experimental setup. (a) Sagittal section of a *P. araujoi* nest showing the foam-like structure and the underground extension of the nest. Yellow or black squares are 5 x 5 cm. (b) *P. araujoi* nest with the monitoring wires. (c) Probe positions inside and around the nests and spatial parameters used in the heat equation. T_1 = Temperature of the top; T_2 = Temperature of the side; T_3 = Temperature of the core; Γ_1 = heat flux between the top and the side probes; Γ_2 = heat flux between the side and the core probes; Δh = height

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63   difference between the time derivative estimation $\frac{\Delta T^n}{\Delta t}$ and the temperature heat flux gradient estimation

64   L_1^n (see text for equations).

65

66   In closed mounds like those built by *P. araujoi*, nest material is likely to influence

67   thermoregulation by affecting the microstructure of the walls and water retention, which

68   are probably also crucial for gas exchange properties in such nests [16,25]. In *P. araujoi,* the

69   workers use soil, regurgitated soil, fecal material and saliva as construction material [21].

70   Moreover, the mounds are often covered by a thin layer of loose soil and grass [20; personal

71   observations] that could also have insulating properties [26].

72   In this study, we monitored nest temperature in different parts of *P. araujoi* nests.

73   Our aim was to characterize the buffering effect of the structure, that is the ability of the

74   structure to regulate the internal temperature against external environmental fluctuations.

75   Previous studies have shown that mounds are subject to daily and long term temperature

76   fluctuations and that termites may contribute to this buffering effect [11,18]. To investigate

77   nest thermoregulation, we propose a methodology that first identifies thermal patterns and

78   then to quantify them using the heat equation.

79   From a technical point of view, detecting patterns in raw time series (as our data) can

80   quickly become tricky [27–29]. Such technical difficulties can obfuscate the actual biological

81   interpretation of the data. Here we first propose to use a quick-look method: rasterization

82   [30–32]. This method consists in transforming 1D time series with a dominant periodic

83   forcing (here daily fluctuation) into a 2D image that can be suitable for a quick visual

84   inspection. In addition we transformed the data by using different thresholding and

85   normalization schemes that allows to accentuate patterns in the rasterized images and thus

86   helping to understand the overall dynamic patterns. This rasterization method first allows us

87   to detect the nests' buffering efficiency at short (daily) and long (across days) scale. We then

88   investigated the physics of the heat transfer dynamics inside the nests in the context of the

89   heat equation. This equation predicts that (a) the mean temperature is independent of the

90   monitored location in the nest, (b) the temperature amplitude decreases with increasing

91   depth (distance to the top of the nest) *i.e.* shows mitigation, and (c) the phase shifts

92   according to depth. A numerical scheme allows to fit the heat equation to the monitoring

93   data. This fit provides two parameters to characterize the mound: the heat diffusion

94   coefficient that quantifies the buffering effect (decreasing amplitude or mitigation), and a

95   constant that tells whether the living mound is globally a free system, an energy source or an

96   energy sink.

97

Methods

Biological material and experimental field area

100   Three nests of the termite *P. araujoi* were monitored during two weeks (04/11/2016-

101   18/11/2016) in a pasture located at the *Fazenda Capim Branco* (18°52'48''S, 48°20'27''W),

102   an area belonging to the Federal University of Uberlândia, Minas Gerais, Brazil (**S1 Fig**). The

103   circumference of each nest at different heights (corresponding to the levels where each

104   probe was inserted (**Figs 1b,c** and **Table S1**)) was measured to estimate the size of the nests.

105   The total volume of a nest was estimated as the sum of the volumes of each section. The

106   volume of the upper section (top of the nest) was calculated using the formula for the

107   volume of a cone ($\pi \times R^2 \times h / 3$, with h the cone height and R the radius at its base). For the

108   2 lower sections, the formula of a truncated cone ($h \times \pi/3 \times (R_1^2 + R_2^2 + R_1 \times R_2)$) was used,

109   where R_1 and R_2 are the radiuses of the upper and lower discs respectively). The total

110   volumes were 0.34, 0.52 and 0.39 m^3 respectively for nests A, B and C (**Table 1**). Taxonomic

111   identification of the termite species was done using the soldier morphology following the

112   dichotomous identification keys of Constantino [33] for the genus and Cancello [34,35] for

113   species identification.

114

115   **Table 1. Nest characteristics.**

Nest	Top of the nest		Top probe entrance		Side probe entrance		Core probe entrance		Basis		
	H	C	H	C	H	C	H	C	H	C	**V**
A	0.72	0	0.6	1.02	0.48	1.77	0.3	2.47	0	4.03	**0.34**
B	0.58	0	0.53	1.3	0.43	2.4	0.25	3.92	0	4.42	**0.52**
C	0.7	0	0.51	1.1	0.4	2.03	0.19	3.27	0	4.7	**0.39**

116

117   Height H (m) and circumference C (m) of the 3 nests at different levels corresponding to the probe entrance

118   points (see Fig 1c) with the resulting nest volume V.

119

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Nest monitoring

Custom made devices (**S1 Text**) were used to measure the temperature every 10 min at five different positions, following Field & Duncan's protocol [18] (see **Figs 1b,c** and **Table S1** for details). Each probe was placed into a 2 cm diameter plastic tube. The tubes were sealed at one end with a mesh to prevent the termites from entering. The other end was sealed with silicone. A concrete drill of 2.5 cm diameter was used to dig the holes into the nest (from the east side) and the ground where the tubes were placed. For each nest, two probes were placed inside each tube at each position in case of failure of one. Probes were placed (1) at the top of the nest, 5 cm below the nest surface, (2) on the side, at a horizontal distance of 20 cm from the surface, (3) inside the core of the nest (40 cm depth with an angle of 45° compared to the horizontal), in the soil next to the nest (4) at 5 cm depth and (5) at 20 cm depth, (6) at 1 m distance from the nest at 20 cm depth. When all the probes were installed, the data-loggers were started. The probes placed at the same location gave quasi identical data (**Table S1**). Therefore, only one of the two probes was used for the analysis.

Environmental parameters (air temperature, solar radiation, precipitations and relative humidity) were monitored in the meteorological station of the *Fazenda Capim Branco* situated approximately at 500m from the experimental field area.

Data visualization: the rasterization method

Rasterization consists in transforming 1D time-series (see different examples of theoretical signals in **Fig 2a**) data into a 2D image by plotting the principal period (*e.g.* day, year, lunar month) on the y-axis, and subsequent periods on the x-axis; the actual signal is encoded in colors to obtain a heatmap like image (**Fig 2b**). Converting a time-series into a 2D image not only allows decomposing the signal, but also applies a smoothing effect that reduces the details and emphasizes the general patterns.

In the case of a weak amplitude of the signal, some patterns can be masked by the color scale (**Fig 2b**). To solve this issue, one can enhance the contrast by normalization of the signal, for example into the range of [-1,1] (see **S2 Text eq (S2)**) (**Fig 2c**). This allows comparing easily the temporal dynamics of signals that have different amplitudes (**Fig 2a** and **2c**).

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151   Another way to enhance contrast and facilitate pattern identification in
152   rasterized images is to use hard thresholding (**Fig 2d**): it replaces each original value by
153   one of two colors (binary data) according to a reference value used as a threshold. This
154   allows to visualize the sign of the anomaly (that is defined as the departure of the value of
155   a series from a reference value).

156   Finally, the dynamics of the time-series can be visualized by plotting the differences
157   between subsequent values in the series (increments). These increments can also be
158   normalized to increase contrast and facilitate pattern identification (**Fig 2e)**.
159   All the plots were done with R 3.2.3 [36] (the dataset and an exemple of the script used to
160   produce the figures are available online (http://doi.org/10.5281/zenodo.822263))

161

162   **Fig 2. Illustration of the rasterization method.** (a) "classical" 1D time-series for different kinds of theoretical
163   signals sampled hourly. The horizontal color bar under the plots represents the encoding of the signal's value in
164   a color scale. Rasterized images of (b) the raw data of the 1D time series, (c) of the normalized data of the 1D
165   time series, (d) of the sign of the departures from a reference value (anomaly), here the mean (values higher
166   than the mean are plotted in magenta and those lower than the mean in blue), (e) of the normalized hourly
167   increments.

168

Dynamical characterization using the heat equation

170   Here we investigate whether the spatio-temporal temperature evolution in the
171   mound can be explained by a simple physical equation such as the heat equation. Using
172   the *in-situ* temperature measurements, a numerical scheme of the heat equation is
173   established in order to check whether this equation is able to predict the temperature
174   inside the nest. This heat equation links linearly the temperature time derivative with
175   the gradient of the heat fluxes. Both terms can be estimated from nest monitoring data if
176   there are at least 3 probes.

177

Mathematical background

179   The heat transfer equation describes the propagation of heat inside a domain. In
180   the context of a termite nest heated by the sun, the heat transfer follows the sunray line.
181   We assume that the heat propagation is done along the vertical axis and therefore that
182   the domain is one-dimensional and semi-bounded. The equation describes the time
183   dynamics of the temperature, represented by the time derivative of the temperature

184   subject to the spatial variation of the vertical heat fluxes with a proportionality

185   coefficient called the diffusivity coefficient.

186

187   The heat transfer is thus the partial differential equation

188
$$\frac{\partial T}{\partial t} = D \frac{\partial^2 T}{\partial z^2}$$

189   that may be also written as

190
$$\frac{\partial T}{\partial t} = \frac{\partial}{\partial z}\left(D \frac{\partial T}{\partial z}\right) = \frac{\partial}{\partial z}(D\,\gamma)$$

191   where T is the temperature (K) as a function of time t and depth z, $T = T(t, z)$, and $\gamma =$

192    $\frac{\partial T}{\partial z}$ (Km^{-1}) is the vertical heat flux. The boundary conditions of the semi-open domain

193   are given by the surface temperature $T_0 = T(t, 0)$. The heat transfer coefficient D is a

194   characteristic of the medium. In the present form of the heat equation, the medium is

195   supposed to be homogeneous and D $(m^2 s^{-1})$ is a constant.

196   The proportionality between the temperature time derivative $\frac{\partial T}{\partial t}$ and the heat flux

197   gradient $\frac{\partial^2 T}{\partial z^2}$ $(K\,m^{-2})$ describes the flow of heat. It is well known that the solution of

198   this equation is a diffusion process. In the case of a sinusoidal surface temperature, an

199   analytical solution of the heat equation is known. We consider that $T_0(t) = T(t, 0) =$

200    $A\,\sin(\omega t) + T_m$ where ω is the pulsation in $rad\ s^{-1}$, A is the amplitude of the sinusoidal

201   function and T_m is the mean temperature. Then the analytical solution is:

202
$$T(t, z) = T_m + A\,e^{-\sqrt{\frac{\omega}{2D}}z}\,\sin\left(\omega t - \sqrt{\frac{\omega}{2D}}z\right)$$

203   The solution of the above equation may be seen as the mean temperature, with an

204   amplitude mitigation function relative to the depth and a phase difference in the sine

205   function given by the depth. It is easy to transform the phase difference into a time lag.

206   Indeed,

207
$$\sin\left(\omega t - \sqrt{\frac{\omega}{2D}}z\right) = \sin\left(\omega\,\left(t - \frac{z}{\sqrt{2D\omega}}\right)\right)$$

208   Therefore, the mathematical solution of the 1D heat transfer equation in the case of a

209   sinusoidal forcing contains the two characteristics seen below in the nest temperature

210   measurements: a time lag and mitigation according to the depth z.

211

212 The heat transfer equation written previously corresponds to a free system. In the case

213 of a non-autonomous system, with an energy well or forcing (such as heat absorption by

214 water brought in by the termites or metabolic heat), the heat transfer equation is

215 modified by an additive term,

216
$$\frac{\partial T}{\partial t} = D\,\frac{\partial^2 T}{\partial z^2} + Q$$

217 The additive energy Q is a negative term in case of a loss of energy, that is an energy

218 sink, and non-negative for an input of energy, that is a positive forcing.

219

Numerical approach

221 In order to link the heat equation to our temperature measurements at few

222 discrete spots in the nest, it is necessary to discretize the partial differential equation.

223 This discretization has to take into account the time characteristic of the cycles

224 according to the time step of the data. It also has to take into account the heat

225 propagation inside the soil. The flux transfer and the heat propagation in the soil are

226 slow processes compared to external temperature forcing. Therefore, before the

227 computation of the time and spatial derivatives, the fast variations are filtered from the

228 temperature measurements by using a Fourier low-pass filter. Since the mean diffusivity

229 coefficient and the mean additive forcing are of interest, the frequency of this low-pass

230 filter corresponds to the diurnal cycle of 24 hours.

231 The time derivative is directly estimated by the first order difference: $\frac{\partial T}{\partial t} \sim \frac{\Delta T^n}{\Delta t}$ where

232 Δt is the data time step, and ΔT^n is the difference $\Delta T^n = T^n - T^{n-1}$ (T^n is the

233 temperature at the time $t^n = n\Delta t$). This temperature derivative series is estimated

234 using the side probe T_2.

235 The vertical temperature Laplacian at a given depth, ΔT is the temperature

236 second derivative. This term is computed by two vertical derivatives. If T_j^n is the

237 temperature for the time $t^n = n\Delta t$ at the j-th depth, the heat flux $\gamma = \frac{\partial T}{\partial z}$ is estimated by

238 $\frac{T_{j+1}^n - T_j^n}{\Delta z_{j+1,j}} = \Gamma_j^n$ where $\Delta z_{j+1,j}$ is the distance between the (j+1)-th and the j-th probes, $j =$

239 1 or 2. This flux is supposed to be estimated at the depth $\frac{z_{j+1} + z_j}{2}$. Using the three

240 different depths, of our temperature measurements possible to compute two fluxes, and

241 the second derivative of the temperature, which is the gradient of the heat flux, is then

8

242   computed with the same method in order to get $\frac{\Gamma_2^n - \Gamma_1^n}{\Delta\lambda} = L_1^n$ where $\Delta\lambda = \frac{z_3 - z_1}{2}$. This term

243   L_1^n is supposed to be estimated at the depth $\frac{z_1 + 2z_2 + z_3}{4}$.

244   The estimates L_1^n have to be corrected by a time shifting (associated to Δh in Fig

245   1c) in order to be adjusted to the temperature increment. Indeed, the distances between

246   the probes are quite large and the time lag is about one hundred minutes per 10 cm,

247   whereas the time step is about 10 min. Therefore a time shifting of the Laplacian

248   estimation L_1 is necessary. Several methods are possible to assess this time shift

249   (Fourier spectral shift, maximum of cross-correlation function, ...). Here we estimated it

250   as the number of time steps that maximize the absolute value of the correlation between

251   temperature derivative $\frac{\Delta T^n}{\Delta t}$ and the heat flux gradient L_1^n.

252   Finally, a linear regression between the time derivative $\frac{\Delta T_n}{\Delta t}$ and the temperature

253   second derivative L_1^n is performed. This regression provides estimates of the mean

254   diffusivity coefficient D and of the mean additive forcing Q. Such a standard linear

255   regression provides also the standard errors of these parameters. However, time series

256   data do not fulfill the independence property assumed in these methods (our

257   temperature time series are highly auto-correlated, leading to underestimated standard

258   errors due to this pseudo-replication). Methods to correct for the bias induced by

259   pseudo-replication are beginning to appear in the statistical literature [37] but their

260   usefulness in the case of time series data is still strongly debated. We therefore chose

261   not to report any standard errors for D and Q in a given nest, but to compute them with

262   the classical formula over the three values obtained for our three (independently)

263   monitored nests.

Results

The mean, standard deviation and coefficients of variation for each probe are given in **Table 2**. The mean temperatures monitored at the different locations of the nest as well as in the soil are almost identical. For both the mound and the soil, the standard deviations decrease with depth z, leading to decreasing coefficients of variation. The temperature amplitudes are indeed much higher at the top of the nest (temperature range [16;44] °C) compared to the core (temperature range [24;28] °C; **Fig 3a, S2 Fig**). The same applies to the comparison of the soil temperatures at 5 and 20 cm. Mound temperatures are on average higher than soil and air temperatures (**Fig 3a**). Note that the air temperature and its amplitude are similar to those of the soil temperatures at 5 cm. In addition, daily variations of air temperature are intermediate between the top and the core of the nest.

Table 2. Descriptives statistics.

	Nest A		Nest B		Nest C	
	Mn ± SD (°C)	*CV*	*Mn ± SD (°C)*	*CV*	*Mn ± SD (°C)*	*CV*
Top	25.82 ± 6.26	0.24	24.39 ± 4.46	0.18	25.54 ± 5.24	0.20
Side	27.00 ± 2.68	0.10	26.63 ± 2.73	0.10	25.89 ± 3.13	0.12
Core	26.42 ± 0.85	0.03	25.79 ± 0.52	0.02	25.64 ± 0.78	0.03
Soil 5cm	23.78 ± 3.42	0.14	NA	NA	23.59 ± 2.43	0.10
Soil 20cm	23.96 ± 1.34	0.06	24.50 ± 1.04	0.04	23.79 ± 0.72	0.03
Air (station)	*Mn ± SD (°C)*	*CV*				
	22.69 ± 3.36	0.15				

Mean (Mn), standard deviation (SD) and coefficient of variation (CV) of the temperature recorded by each probe for the 3 nests and for the air (meteorological station) during the 14 days. NA corresponds to the case where both inserted probes failed.

Fig 3. Rasterization raw data (transform 1D time-series into a 2D image). (a) for the 3 nests and all the probe positions and (b) for the environmental parameters (air temperature, solar radiation, precipitations and relative humidity). White space indicates missing data.

Interpretation of the rasterized images

The rasterized images of the raw data (**Fig 3a)** show comparable patterns for probes at the same location in the three nests. In addition to the decreasing amplitudes (mitigation)

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289   with increasing depth in both the nest and the soil, data also show that maximum

290   temperatures are attained later in the evening with increasing depth (Fig 3a). However, on

291   these figures one can barely see a pattern in the core or soil at depth 20cm. A clear pattern

292   appears in both cases in **Fig 4** where we normalized the data into the range [-1;1]; maximum

293   temperatures were much delayed compared to air and nest top ones (around 4 pm),

294   occurring at midnight in the core. One can also see that the highest temperatures and the

295   daily variation are smaller in all probe locations on days 11 and 12. This can be explained by

296   cooler air temperature, less intense solar radiation and higher precipitations (with higher

297   relative humidity, see **Fig 3b**) for these two days. This reveals that temperature of the nest

298   follows the long-term environmental fluctuations and is true even for the core temperature

299   although more attenuated than at the most peripheral locations in the nest and in the soil.

300

301   **Fig 4. Normalized rasterized data.** Data illustrated in Fig 3 (raw data) were normalized to restrict the values

302   into a range of [-1;1] (see equation S1).

303

304   **Fig 5** shows the differential sensitivity of the upper part of the mound (top and side)

305   and of the nest core to environmental fluctuations as revealed by the sign of the global

306   anomaly of the time-series. The dominant vertical pattern seen in the core indicates that this

307   latter is mainly sensitive to larger-scale external temperature changes while the dominant

308   horizontal pattern seen in the top and side of the mound are more sensitive to the diurnal

309   variation of the temperature. The pattern of anomaly shown in the soil at 5 cm and 20 cm

310   depth are respectively quite similar to the ones observed at the top and the side of the nest

311   showing that it follows principally daily fluctuations. The pattern of the side and soil at 20 cm

312   reveals an intermediate pattern between the core and the surface (top of the mound and

313   soil at 5 cm). Indeed, this pattern reflects both short (daily) and long (across days) term

314   fluctuations. The relative long term fluctuations of the top and the side of the nest as well as

315   of the soil at 5 cm can be visualized through the sign of the anomalies using the hourly mean

316   temperature as threshold value (**Fig 6**).

317

318   **Fig 5. Rasterized sign of the anomalies using the overall mean as the threshold.** The positive anomaly is

319   indicated in magenta and the negative anomaly in blue.

320

321 **Fig 6. Rasterized sign of the anomaly using the hourly means over the two weeks of observation period as**

322 **the reference thresholds.** The positive anomaly is indicated in magenta and the negative anomaly in blue.

323

Dynamical characterization

Visualizing the heating and cooling phases

326

327   To visualize the temporal dynamics of heating and cooling, we plotted the hourly

328 mean raw temperature at the different locations for the three nests (**Fig 7a**). We excluded

329 days 11 and 12 which were different from the other days (**Fig 3**). The normalization of this

330 data reveals a temporal shift of the maximum and minimum temperatures as one goes

331 deeper inside the nest or in the soil (**Fig 7b**). Remarkably the heating and cooling of the core

332 follows an inverted temporal pattern when compared to the top of the nest. Nevertheless, it

333 is not easy to perceive whether the duration of the heating or the cooling are the same. This

334 is easier to assess on the rasterized image of the normalized temperature increments

335 following **eq S1** (**Fig 8**). The heating phase is well identified by the dominant magenta

336 coloring, while the cooling phase has dominant blue coloring. Whatever the location, the

337 heating phase is shorter than the cooling phase. We also notice that these two phases

338 tended to be less asymmetric the deeper the probe location. The alternating pattern of 0

339 and of non-zero values in the least-varying core temperatures illustrates rather slow periods

340 of heating and cooling (see **eq S1**). By contrast, the almost continuous color patterns at the

341 top and the side of the nest indicate faster heating and cooling periods preceded or followed

342 by a rather long period of stationary temperatures centered around midnight.

343

344 **Fig 7. Mean temperatures along a 24h period.** (a) Mean temperatures during the day after excluding days 11

345 and 12. (b) Normalized curves (between [-1 ;1]) of the same mean temperatures.

346

347 **Fig 8. Rasterized increments of the raw data.** The amplitudes of the increments ΔT^n are normalized to restrain

348 the values into a range of [-1;1].

349

Nest diffusivity coefficient

351 **Fig 7. Estimation of the temperature time derivative ($\frac{\partial T}{\partial t}$) and the flux spatial gradient ($\frac{\partial \gamma}{\partial z} = \frac{\partial^2 T}{\partial z^2}$) for nest A.** (a)

352 time derivative as a function of the flux spatial gradient, with the best fitting line (red) to estimate the

353   diffusivity coefficient D and the energy source Q, (b) the time derivative and its linear prediction from the

354   spatial flux gradient as a function of time, (c) the residuals of the linear regression in (a) as a function of time.

355

356   **Table 3. Estimated diffusivity coefficients and forcing terms in the three nests.**

Nest	Diffusivity Coefficient $D\times10^{-6}(\mathrm{m^2 s^{-1}})$	Forcing term $Q\times10^{-4}$ (K/ s)	Adjusted R2	$\Delta z^{2,1}$ (m)	$\Delta z^{3,2}$ (m)	Time shift (min)
A	0.27	0.41	0.94	0.12	0.39	80
B	0.35	1.22	0.88	0.10	0.39	90
C	0.80	0.40	0.88	0.11	0.42	170
mean±se	0.47 ± 0.16	0.68 ± 0.27				

357

358   The Δz are the vertical distances between the probes and the time shift is the one used in the estimation of

359   the heat flux gradients L_1^n

360

361   **Fig 9a** shows the relationship between the time derivative and the spatial flux derivative for

362   nest A; the data are organized along a flat ellipse, a linear regression thus makes sense. The

363   associated residual structure in **Fig 9c** confirms this conclusion. **Fig 9b** shows the time

364   derivative and its linear prediction from the spatial flux gradient: there is a good agreement

365   between the two series. The two other nests give quite similar plots.

366   The estimated parameters of the heat equation for the three nests are summarized in **Table**

367   **3**. Nests A and B have coefficients of the same order, with $D\sim0.31 - 0.51\ 10^{-6} m^2 s^{-1}$. Nest

368   C's diffusivity coefficient is doubled. The mean additive forcings Q are all positive and in the

369   range $0.37 - 1.24\ 10^{-4} K s^{-1}$. The time lag is about 70-80 minutes for nests A and B, and

370   about 170 minutes for nest C. In conclusion, nest C seems to have a behavior different than

371   the two other nests.

Discussion

373   Termite mounds are historically cited as an example of thermoregulated

374   constructions [6]. Nevertheless, recent studies rather suggest that there is no active

375   thermoregulation in these structures, even in the complex mounds of the fungus growing

376   termite *Macrotermes michaelseni* [7]. Here, we measured temperature at different positions

377   in the nest of the Neotropical mound-building termite *P. araujoi*. We aimed to characterize

378   the dynamics of heat propagation and to investigate how the structure reacts to external

379   forcing. We first used rasterized images to visualize our data and to decompose the effects

380   of the diurnal and the large scale temporal forcing on temperature in the different parts of

381   the nest. The results show that nest temperatures are strongly correlated with external

382   forcing (solar radiation, rain), an argument for the weakness or absence of active

383   thermoregulation. Nevertheless, even these simple homogeneous foam-like architectures

384   show interesting thermal properties. Our results show indeed that the temperature pattern

385   of the mound core differs from the top and the side of the mound as well as from the soil

386   (both at 5 cm and 20 cm depth). On the one hand the core temperatures are very stable on a

387   daily scale, while there are more important temperature fluctuations for the rest of the

388   mound and the soil (**Fig 3** and **Table 2**). They are also higher than in the soil, thus providing a

389   warm and very stable environment for the termites. On the other hand, it is also clear that

390   the core, like the other parts of the mound and the soil, undergoes long term variations as

391   the pattern observed for the core in Figs 4 and 5 corresponds to the one observed for the

392   meteorological data (**Fig 3b**). These results confirm the findings on the mounds of the

393   African termite *Trinervitermes sp*. which builds nests with similar architecture [18,19]. In

394   particular, the increased core temperature has been found during the whole year [18] and is

395   thus not only a simple consequence of monitoring temperature during the summer as we

396   did.

397   From a functional point of view, the stable and warm temperature of the nest core

398   might have significant effects on individual and colony development. Termites are

399   hemimetabolous insects that undergo successive molting events during their life. In

400   particular, during the post-embryonic development of termitid species, such as *P. araujoi*,

401   the larvae follow one of either the apterous line, from which workers and soldiers originate,

402   or the imaginal line from which alates originate [38]. Stable temperature may accelerate the

403   rate of juvenile development [39], as it is the case in the nursery chambers of the nests of

404   Macrotermitinae species (reviewed in [2]). Temperature can also influence caste

405   composition [40,41]. Temperature variations may thus have a strong impact on the colony

406   homeostasis which is based on the division of labor between the different categories of

407   individuals which perform different behavioral activities [42].

408   In contrast to nests of *T. trinervoides* [18] our species' nests extend below ground. A

409   comparison between the core and soil temperature dynamics is therefore relevant. Though

410   the patterns observed for the core are relatively similar to the ones for the soil at 20 cm

14

411   depth, there are strong differences between the two concerning the dynamics of cooling and

412   heating (**Figs 7** and **8**). The heating phase occurs later in the core compared to the soil. This

413   could be explained by the fact that it takes much more time for the heat to propagate from

414   the top of the mound which lies at 60-70 cm above the soil, than it takes to propagate from

415   the soil surface to the 20 cm depth probe. Moreover, in the increments plot (**Fig 8**) one can

416   see that the spacing between the discrete lines during the heating phase is tighter in the soil

417   than in the nest's core, showing clearly that the latter has more efficient buffering properties

418   against external forcing. Compared to the soil, the mound core therefore provides a more

419   stable (and warmer) environment for the termites. Note that temperature increments are

420   negatively correlated with spatial temperature variation between probes (**Figs 4** and **8**),

421   indicating that it is relevant to analyze nest temperature dynamics in the context of the

422   general heat equation. In fact, our analysis suggests that the heat equation explains well the

423   diffusion of heat inside the mound structure. Our estimation of the heat diffusivity

424   coefficients are similar to those of soils of similar composition [43]. The higher diffusivity

425   coefficient and time shift of nest C (Table 3) could be natural variation in our small sample or

426   the particular position of this nest at the base of a steep slope in the field (Fig S1). To further

427   investigate the effect of architecture or topographic environment on heat diffusion the

428   mound and soil diffusivity should be compared in a paired design (at least 3 probes in both

429   the nest and the adjacent soil) with more monitored nests. Bristow *et al* [11] had already

430   used the heat equation to detect an energy sink in the mound-building termite

431   *Tumulitermes pastinator*. Our numerical scheme goes significantly further in terms of model

432   validation, precision and parameter estimation. The results obtained in *T. trinervoides* [18]

433   suggest that mound temperature is increased in the presence of termites. However, simple

434   metabolic heat has been ruled out in the case of *M. michaelseni* [7] which, as a fungus

435   growing termite, produces much more metabolic heat than *P. araujoi*. An increase in

436   temperature could be induced more actively by the termites [44] or by the mound design

437   itself. Whatever the origin of this additional source of energy, our methodology permits to

438   precisely quantify its value.

439   We think that the methodology we proposed here could be useful for future studies

440   aiming to understand the mechanisms underlying termite nest thermoregulation. From a

441   physical and evolutionary point of view a comparative approach between sympatric species

442   that only differ by their mound architecture would be particularly interesting. In the case of

443 *P. araujoi* we suggest to compare to *Cornitermes cumulans* (whose individuals are close in

444 size but whose mound architecture is much more elaborated with solid outer walls and soft

445 organic inner space [45,46]) or to *Cornitermes bequaerti* (whose mounds are not closed but

446 have outside openings for ventilation [46,47]).

447   To conclude, rasterization allowed a quick assessment of temperature monitoring

448 data, suggesting the heat equation could govern nest temperature dynamics. The

449 parameters of the heat equation were estimated from the monitoring data in order to

450 characterize the overall nest temperature dynamics. To our knowledge this is the first study

451 that develops a numerical scheme to link the heat equation to mound temperature

452 dynamics and thus validates its pertinence for the studied system.

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Author contributions

459 RG, RB, VF and CJ designed the experiments. RG, VF and IH did the field work. IH provided

460 field support. PA designed and constructed the data logger. RG, CB and CJ did the data

461 analyzes and wrote the manuscript. All authors discussed and commented on the

462 manuscript.

Competing financial interests

464 There are no competing financial interests involved in this paper.

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591
592
593

Supporting Information

594

595 **S1 Text. Data loggers.** Data loggers are designed to work autonomously for several weeks. They store
596 temperature every ten minutes on an SD card (Secure Digital). The data logger has 3 main parts:

597 - 10 sensors measuring temperature (SHT25, Sensirion AG, Staefa ZH, Switzerland)
598 - Mass storage (2GB micro SD card, Transcend Information - Inc., Taipei, Taiwan)
599 - Microprocessor (PIC18F26K22, Microchip Technology, Chandler, Arizona, United States)
600 The processor coordinates the actions via an internal clock activated every ten minutes. It sequentially
601 accesses each of the ten sensors, reads the temperature and stores these ten values in an internal RAM
602 (Random Access Memory). Every 40 minutes, data in RAM are converted to ASCII (American Standard
603 Code for Information Interchange) and then saved on the SD card in a standard CSV format (Comma-
604 Separated Values). This implementation contributes to the long autonomy of the device. The data is coded
605 on sixteen bits (maximum 65535 or five ASCII characters). The fourteen most significant bits represent
606 the measured value and the two least significant bits contain status information that is not used here.
607 These two bits must be set to zero for the calculation of temperature detailed below. Temperature T (S_T in
608 binary format) is obtained through the transformation:

609
$$T = -46.85 + 175.72 \left(\frac{S_T}{2^{16}} \right) \qquad (S1)$$

610 According to the SHT25 datasheet, the accuracy tolerance of the sensor is +/- 0.2°C in the normal range of
611 use. For further energy economy the resolution of the analogue-to-digital conversion was chosen on 11
612 bits (faster reading times), which allows a resolution of approximately 0.08 °C (linearized values).

613

614 **S1 Table. Differences between homologous probes.**

615

	Probe	Mean diff (°C)	SD diff (°C)
	Core	-0.056	0.043
Nest A	*Side*	-0.056	0.043
	Top	-0.056	0.043
	Core	0.063	0.11
Nest B	*Side*	0.063	0.11
	Top	0.063	0.11
	Core	0.01	0.092
Nest C	*Side*	0.01	0.092
	Top	0.01	0.092

616

617 For all the nest positions, two probes were placed in the same tube. We calculated the mean and standard
618 deviation of the differences for each of these pair of probes for the 3 nests.

619

620 **S2 Text. Data normalization.** The data presented in **Figs 1e**, **1f** and **1i** were normalised using the
621 following formula:

21

622
$$xnorm_i \; = \; 2 * \left(\frac{x_i - x_{min}}{x_{max} - x_{min}} \right) - 1 \quad \text{(S2)}$$

623   After applying this transformation, the new data values $xnorm_i$ are bound between -1 and 1.

624

625   **S1 Fig. Experimental field area.** The labels indicate the nest positions in the field. The line A/A' indicates

626   a sagittal section of the field (inset) showing the slope and altitude difference between the nest C and the

627   two other nests (A and B). Map data © 2017 Google, Imagery © 2017, CNES/Airbus, DigitalGlobe.

628

629   **S2 Fig. Raw time series data for the 3 nests.** The lines are the raw temperatures as a function of time for

630   the different probe locations.

631

632

633
634

635

a **b** **c**

a

Top	Side	Core	Soil 20cm	Soil 5cm	
					Nest A
					Nest B
					Nest C

b

Air temperature · Solar radiation · Precipitations · Relative humidity

a

Nest A — Nest B — Nest C

Legend:
- Air
- Top
- Side
- Core
- Soil 5cm
- Soil 20cm

Y-axis (top row): Mean temperature (°C)

b

Y-axis (bottom row): Normalized mean temperature

X-axis: Time (hour)

a **b** **c**

Section

Nest C

Nest B

Nest A

15 m

A   A'
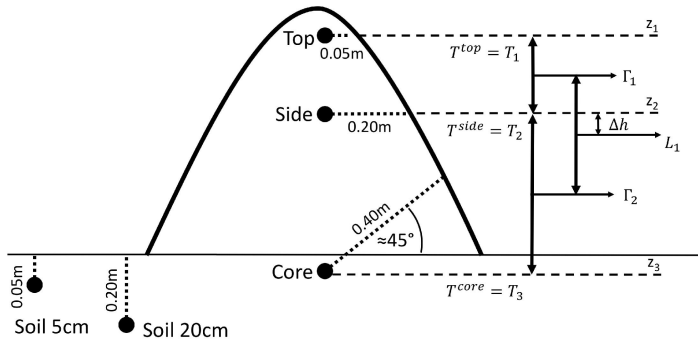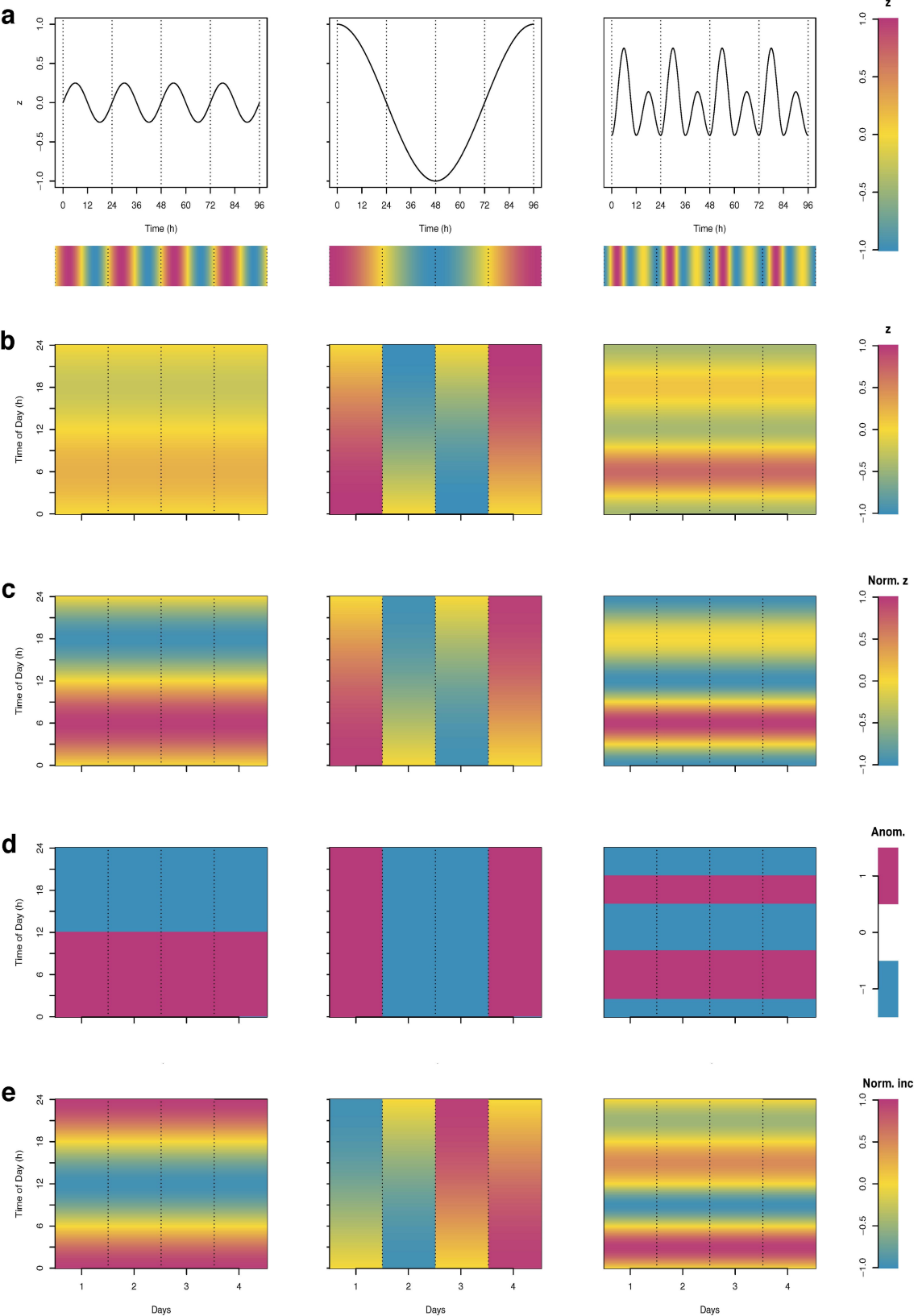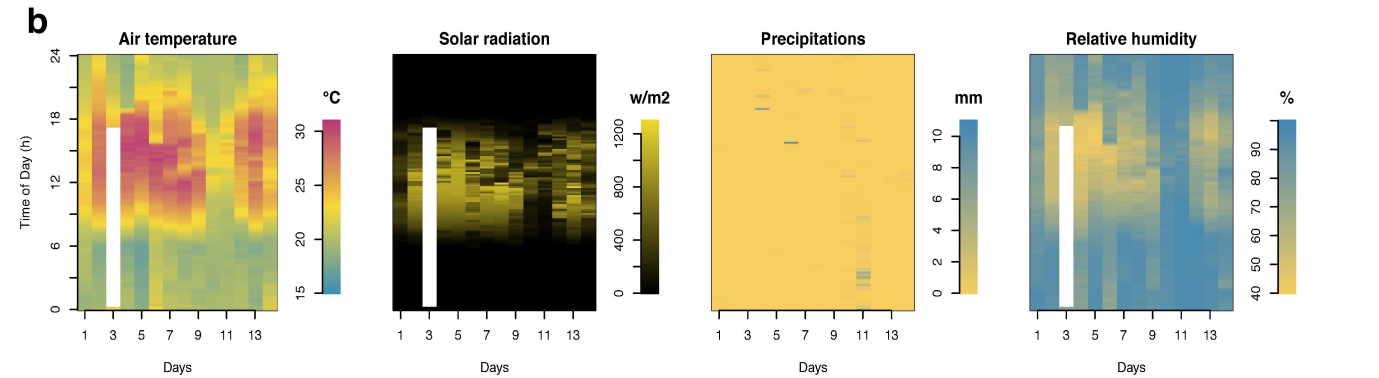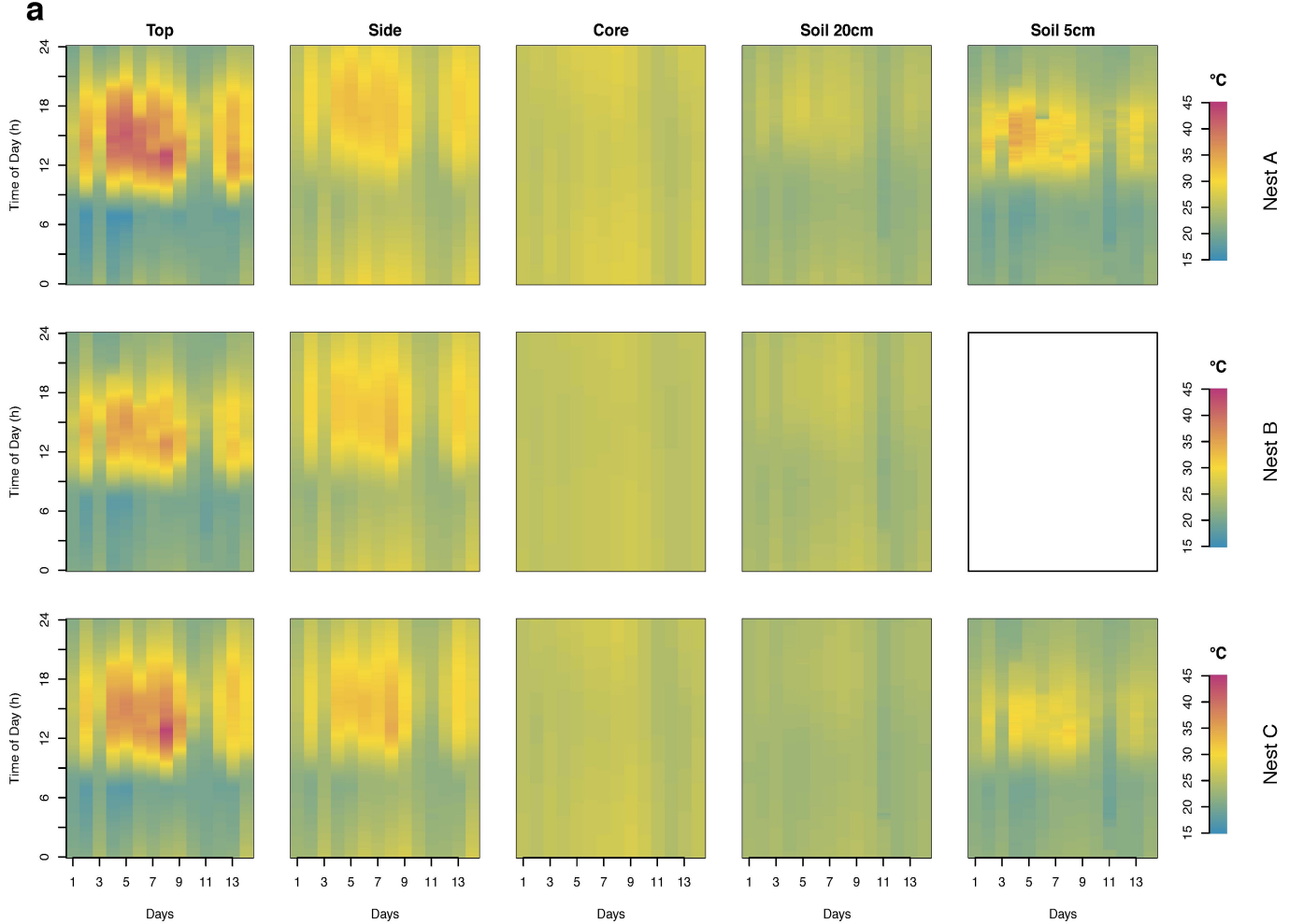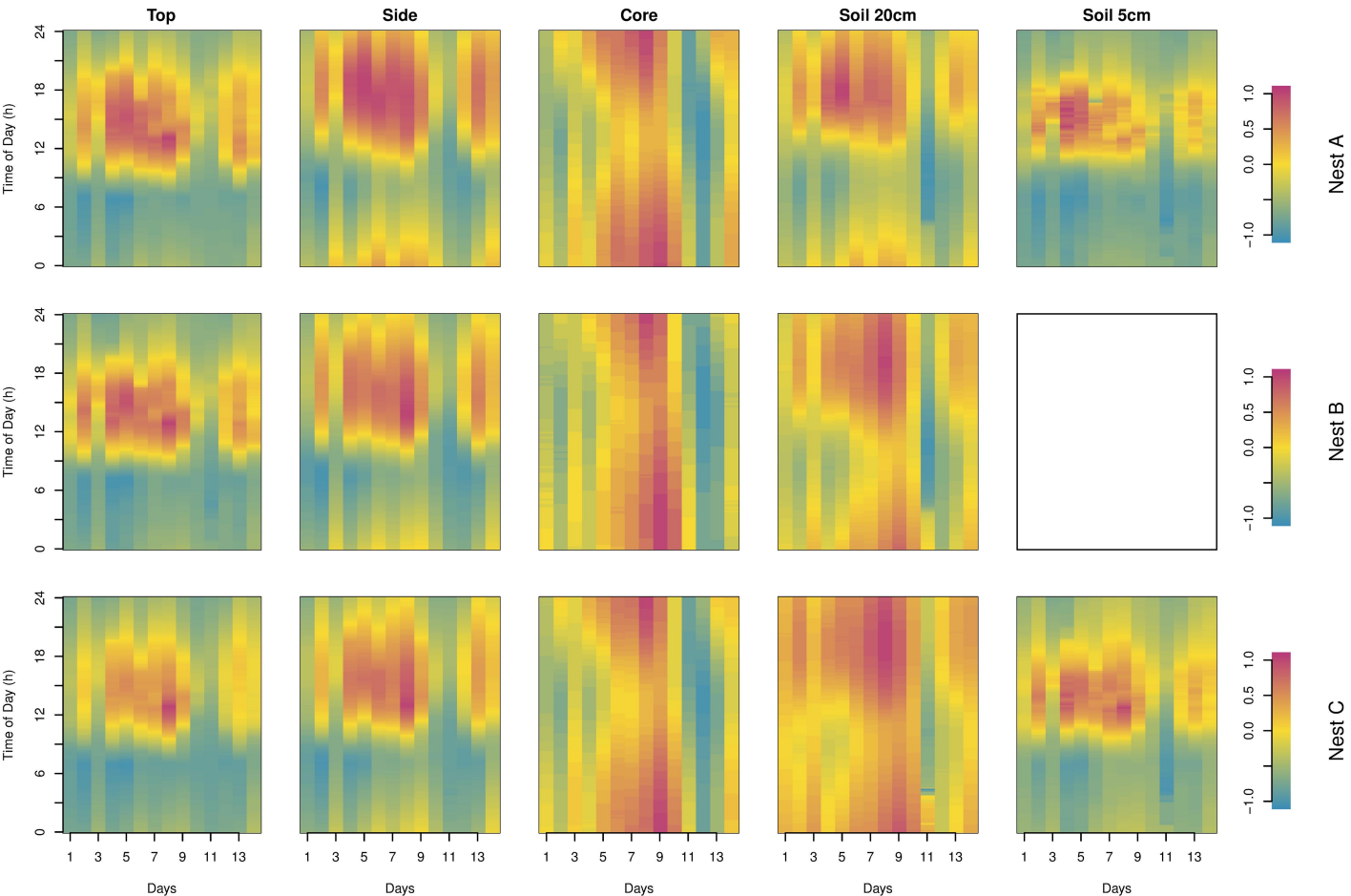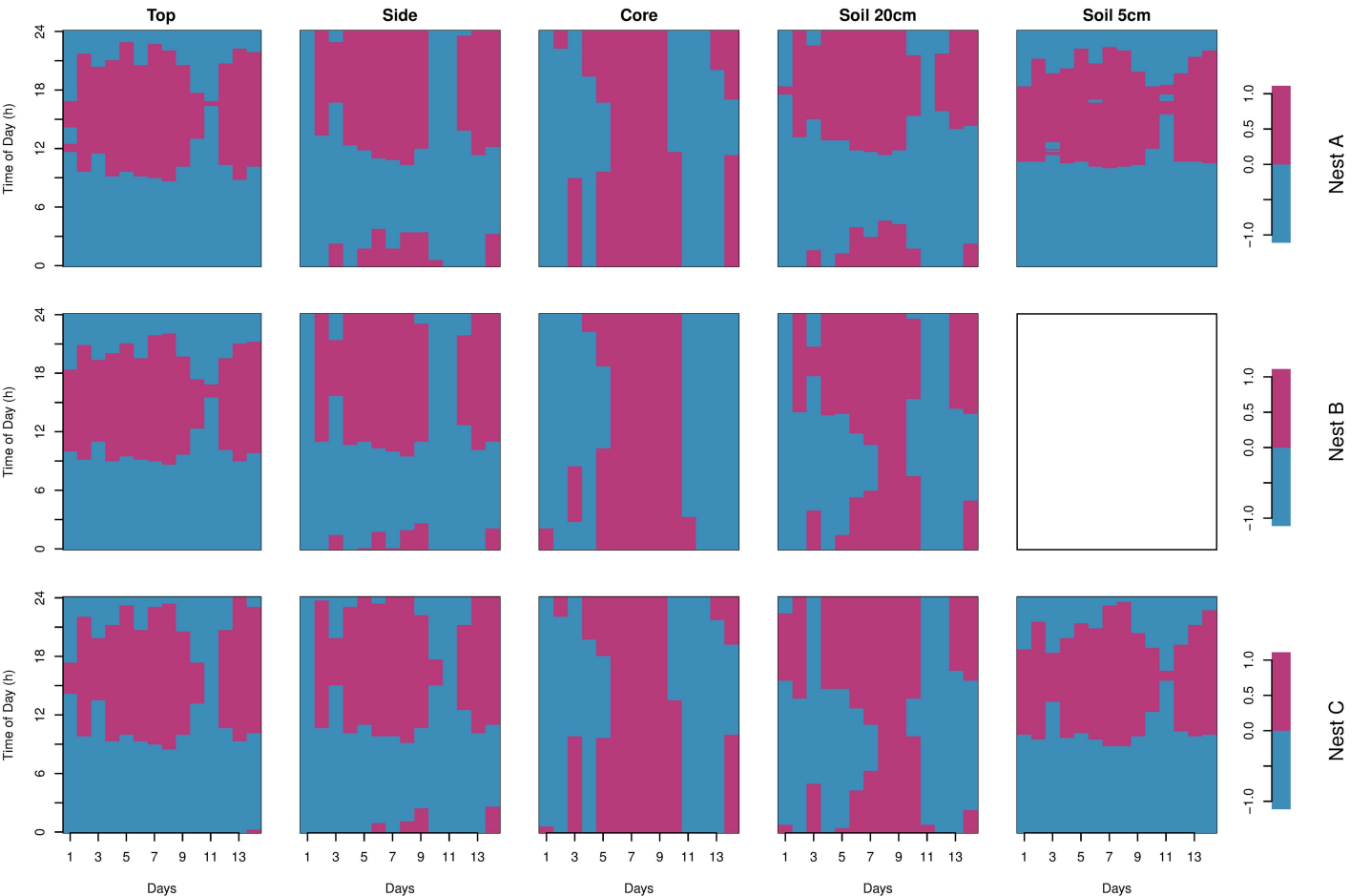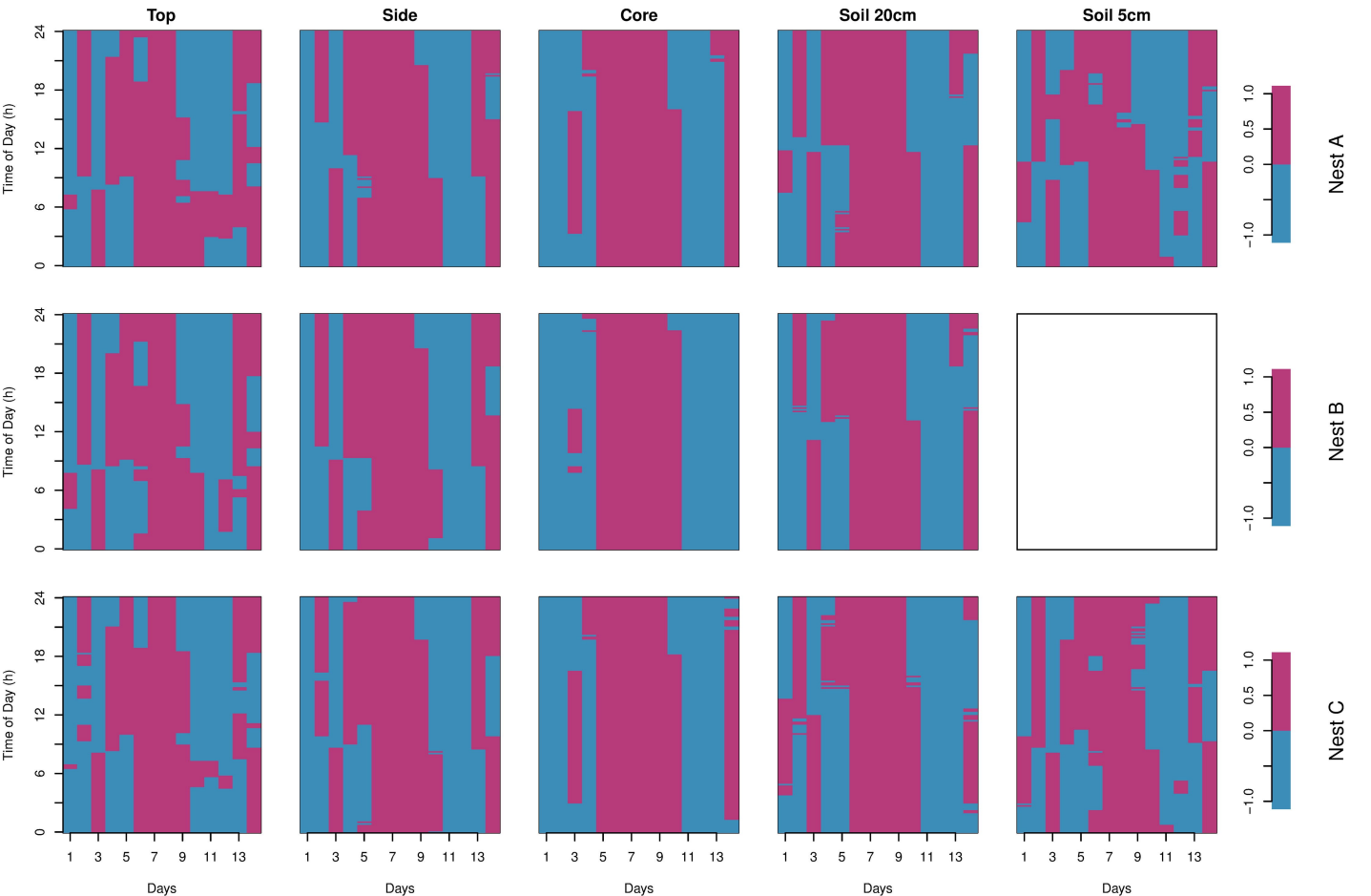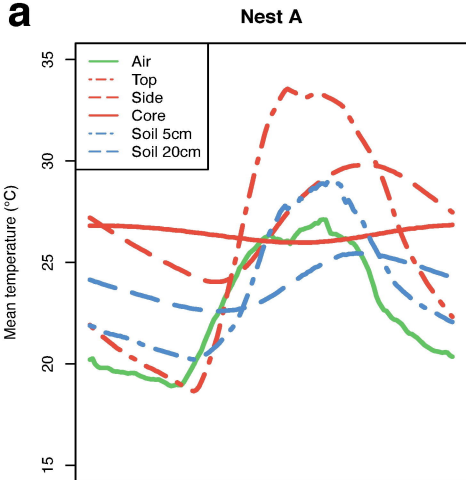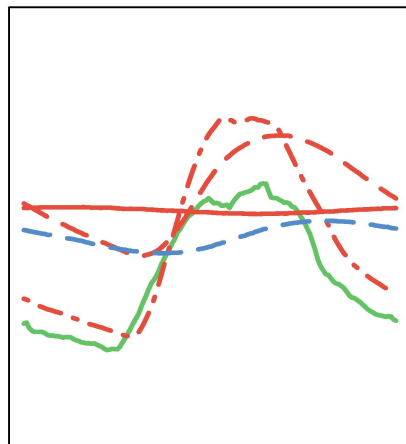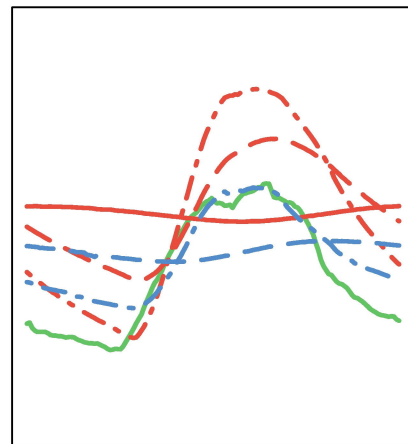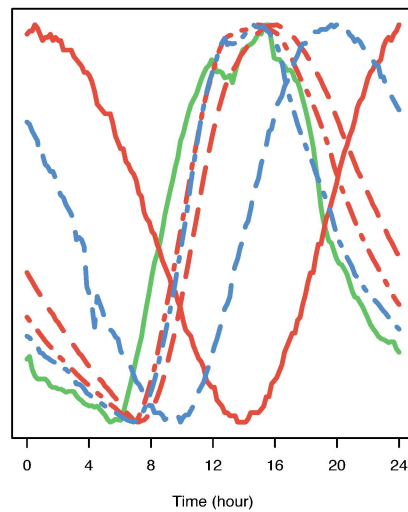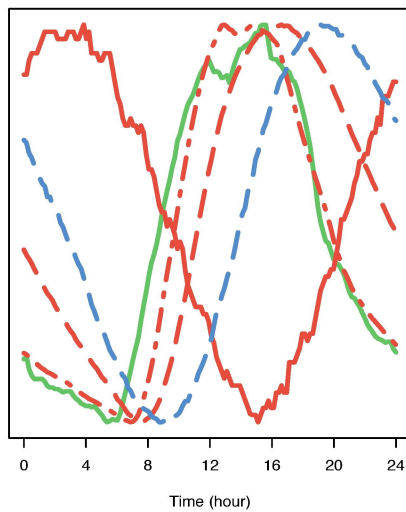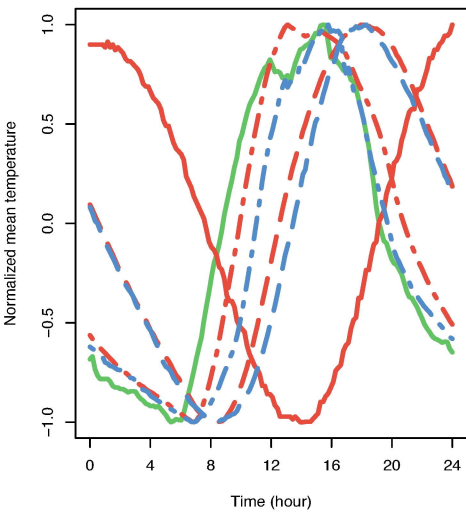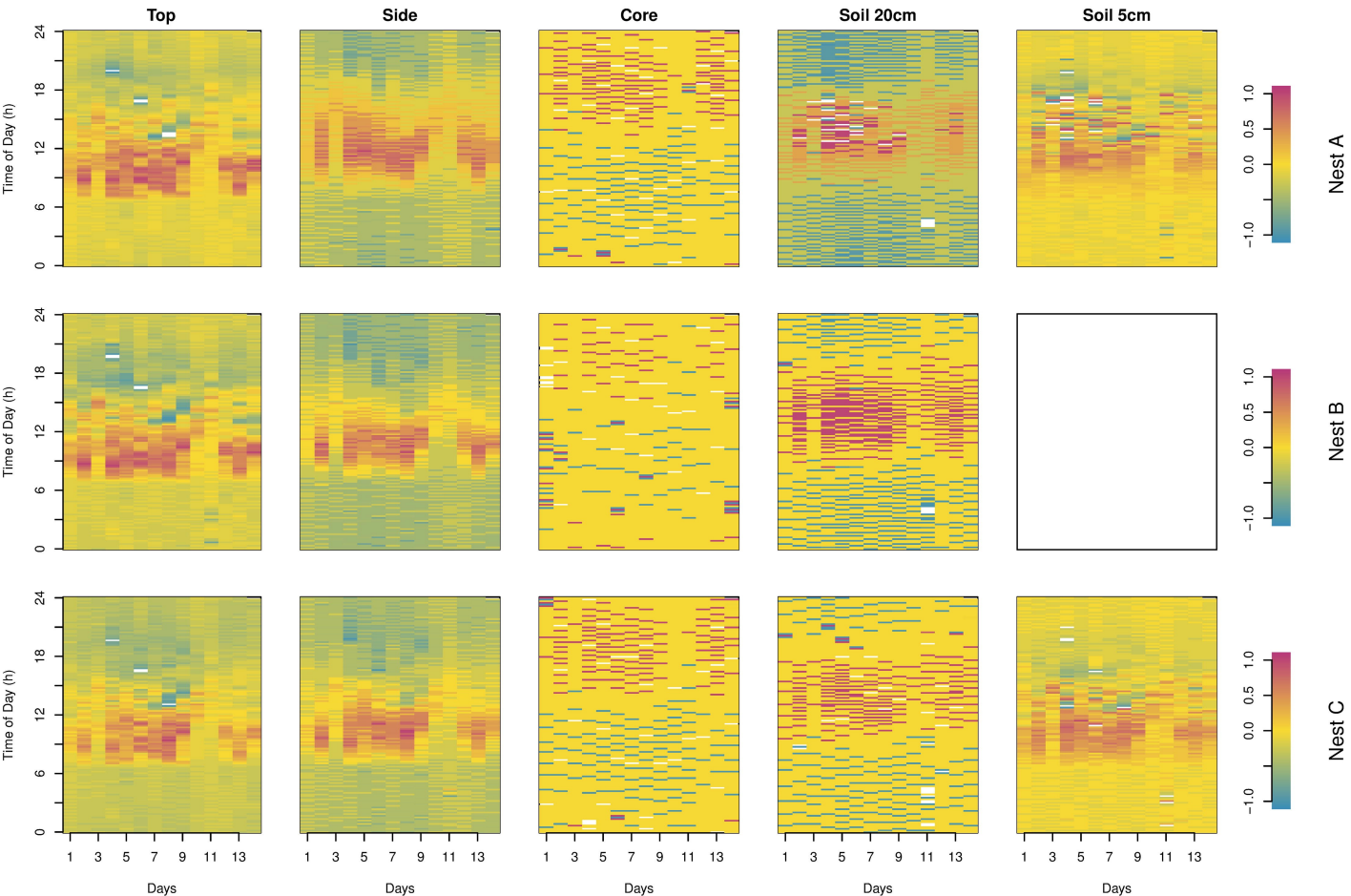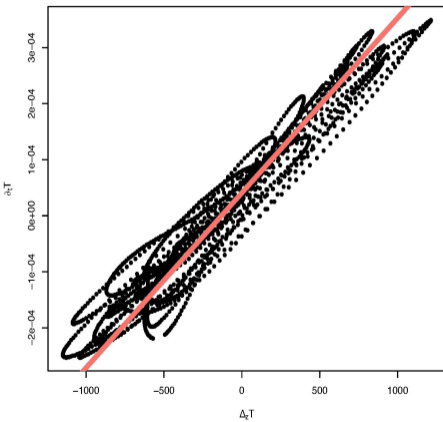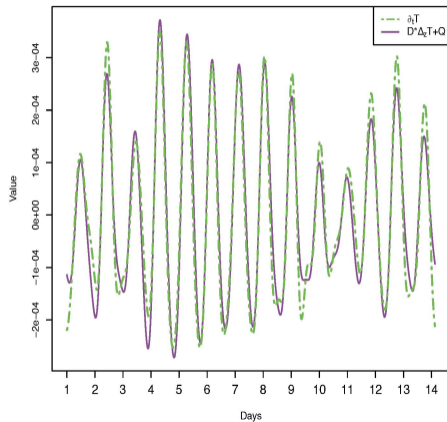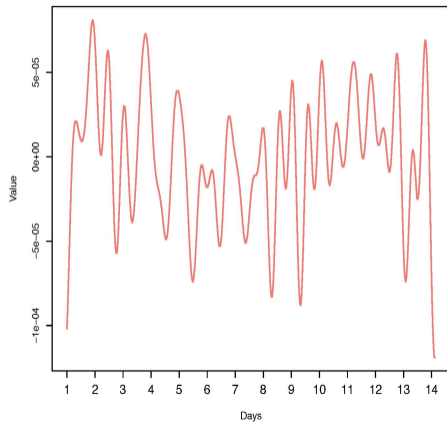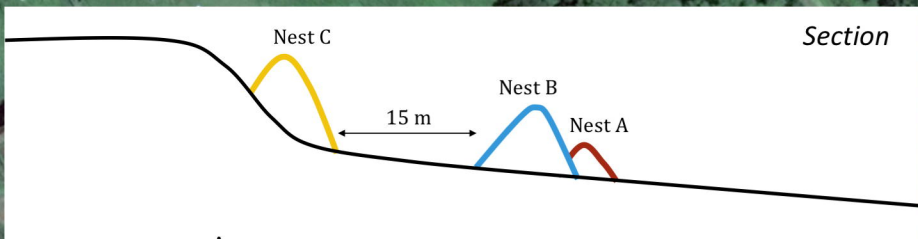
Nest   A
Nest   B
Nest   C
Meteorological station

A'

Section

A

100 m

Map data ©2017 Google, Imagery ©2017 CNES / Airbus, DigitalGlobe

Nest A

Nest B

Nest C