

A simple graphical method for displaying structured population dynamics and STdiag, its implementation in an R package

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Abstract

In demography, a detailed study of the temporal dynamics of the structure of a population is often required to better understand the processes that underline its overall dynamics and the individual's life histories. Heatmaps, using time and structure (such as size-structure) as x and y coordinates and density as colours, are efficient tools for displaying the dynamics of a structured population. Such representations (structure-time diagrams) reveal the data at several levels, from general outlook to fine details. Despite its efficiency, this type of visual display has been scarcely used in ecology and demography. Using the example of springtail populations maintained in the laboratory and a woodlouse population studied in the field, we explain why this type of representation can be used to analyse the population dynamics of soil organisms and why it should be more widely used in demography. We also present the R package STdiag (for 'Structure Time diagram'), an interface to complex graphical functions to easily produce and analyse such 'structure-time diagrams' from raw datasets. This package is available for all operating systems via R-Forge. Its syntax and options are described, discussed and illustrated using our case studies. This graphical display is a simple and efficient way to make large demographic datasets coherent and to disclose the underlying, often hidden, demographical processes.

Keywords Demography | temporal dynamics | long-term studies | graphical display

1. Introduction

Structured populations are complex assemblages of individuals differing in age, size or body condition, reproductive stage or physiological state. The dynamics of structured populations are often complex, hard to keep track of and difficult to understand and analyse (Benton et al. 2006). Depending on their state, size and age, the individuals have different demographic performances and respond differently to ecological mechanisms such as competition or to environmental factors such as resource or temperature. Furthermore, population structures are shaped by the complex interplay of both biotic and abiotic effects (Ohlberger et al. 2013). For

an individual, the effect of the demographic feedback loop depends on the state of the individual itself but also on the structure of its population. For instance, if large individuals dominate the smaller ones through interference competition in a population, the strength of the competition perceived by an individual is determined in a complex manner by its own body size and by the size-structure of the population (Le Bourlot et al. 2014). The demographic responses to environmental change can also be non-trivial, because the sensitivity of the individual's demographic performances to an environmental effect may differ depending on the state, age or size of the individuals (Ohlberger et al. 2011). A gradual change in temperature can, for example, suddenly destabilise the

population dynamics, which can shift abruptly towards a new regime (Oehlberger et al. 2011, Nelson et al. 2013). This complexity is increased again by the fact that the dynamics of a structured population is influenced not only by the current biotic and abiotic conditions, but also by long-term effects due to long-lasting effects of previous environmental conditions (Baron et al. 2010, Mugabo et al. 2010) and to inter-generational effects (Benton et al. 2008, Marquis et al. 2008).

Given the multiple causes that influence population dynamics and the complexity of the direct and indirect mechanisms through which they drive the population dynamics, we argue that extracting relevant biological information from structured population time series

requires not only fitting complex demographic models to the data, but also studying graphs of the population structure dynamics, which can themselves contribute to understanding what happens in the population. When used on their own, models and calculations can be misleading since they rely on assumptions that may be false. A good graphical display can reveal, without distorting, what the data have to say (Tufté 2001). Graphs can be very valuable for studying the data at several levels of detail, to look for signatures of past conditions on the dynamics, to verify the validity of the model's assumptions and even to suggest alternative ways of setting up the statistical analysis (Anscombe 1973). The aim of this paper is to present a simple graphical method

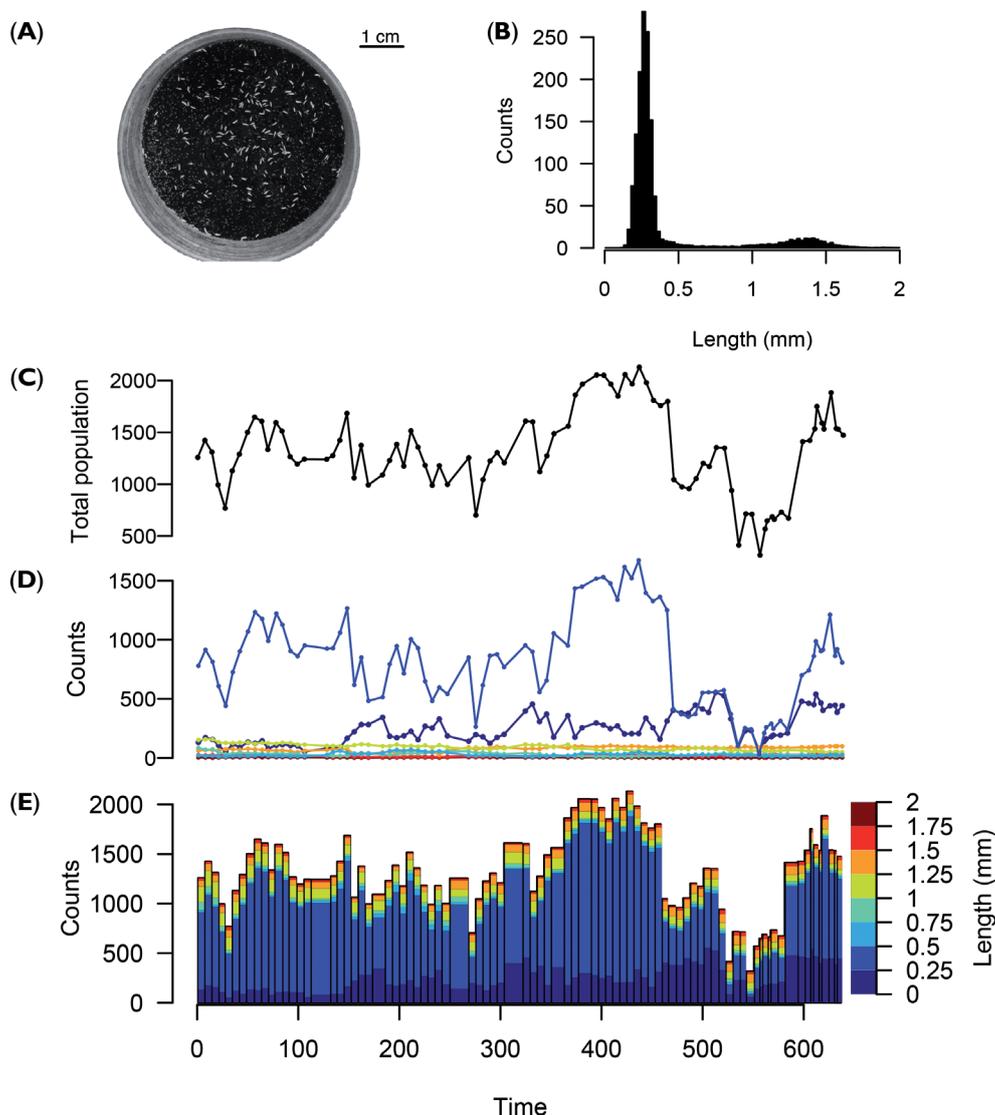


Figure 1. As a practical example, we used an experimental population of the Collembola *Folsomia candida* (A), whose structure had been measured every one or two weeks. The size structure at one time is classically shown as a histogram (B) and the total population dynamics on a time series plot (C). To represent both the structure and temporal dynamics, the population has been divided in several size classes to plot their dynamics independently (D) or to produce a stacked bar plot (E). While these representations underline the dynamics inside each size classes, the patterns of dynamics between adjacent classes remain hidden.

for displaying the temporal dynamics of structured populations, which can be used to visualise large and complex demographic time-series efficiently, revealing the details and nuances of the complex demographic processes that occur in most populations. We argue that such graphical displays are essential tools for ferreting out the devils hidden in the details of structured population dynamics (Benton et al. 2006).

Different approaches have been used to display structured population dynamics (Fig. 1C, D, E). First, by displaying the whole population size fluctuations, the structure is then not taken into account (Fig. 1C) (Schrautzer et al. 2011). Refining a little bit, the structure can be roughly considered by splitting individuals into separate groups (of size or stages), whose dynamics can be displayed on adjacent plots (Plaistow & Benton 2009) or, to facilitate comparisons, on overlaid curves (Fig. 1D) or on a stacked bar plot (Fig. 1E) (Madsen & Shine 2000). Condensed three-dimensional diagrams are required to finely display the structure dynamic, especially when the structuring factor is continuous (size, age). These diagrams encompass ‘event history diagrams’ that allow the graphical representation of life history traits at the individual level of a whole cohort (Carey et al. 1998, 2008) or the production of ‘shaded contour maps’ such as the ones used to represent the temporal dynamics of aged-structured demographic rates (also called ‘Lexis diagrams’) such as death or birth rates in human populations (Vaupel et al. 1997, 1998). These graphical representations are mainly used in human demography to represent secular changes in age-dependent demographic rates (Vaupel et al. 1987, 1997, 1998, Andreev 2000, Erlangsen et al. 2003). To our knowledge, despite their interest, such powerful visual display tools have almost never been used in ecology to represent the temporal dynamics of structured populations (Færøvig et al. 2002). This may result from the prohibiting cost of publishing colour pictures. With the development of online publishing, colour methods are becoming more widely used. The R software (The R Development Core Team 2012) is a language and environment for data manipulation, calculation, statistical computing and graphic display. Heatmaps can be produced using base packages (e.g. `image` in `graphics` and `heatmap` in `stats`) or using specific libraries such as `lattice` (Sarkar 2008) or `ggplot2` (Wickham 2009). Although highly customizable, the plotting functions are often difficult to handle for beginners.

We developed the R-package `STdiag` to provide a user-friendly interface for representing time series of structured populations using heatmaps. This package has been originally designed to study the dynamics of springtail populations that we maintained in our

laboratory. It can be applied to other soil organisms and also to many other case studies. We therefore detail how to generate such graphics and discuss their biological interests focusing on two case studies.

2. Material and methods

2.1. Method overview

Our method produces diagrams that we refer to as ‘structure-time diagrams’, with a structuring element (age, size, ...) along the Y-axis and time along the X-axis. These variables are usually continuous but are discretised in a histogram and put into several classes, the number and width of which depend on the quality and size of the available dataset. For each time and structure class coordinate, a colour rectangle is plotted whose hue refers to the number of individuals (or any other relevant statistics such as frequency or rate) in that class (possibly on a logarithmic scale) at the given time. This representation puts side-by-side colour histograms for each time value and emphasises the temporal dynamics according to the structure of the population.

2.2. Empirical data

We applied our graphical representation method with the help of the `STdiag` package to two soil organisms, the springtail *Folsomia candida* Willem, 1902 (Collembola, Isotomidae) and the pill woodlouse *Armadillidium vulgare* (Latreille, 1804) (Isopoda, Armadillidiidae).

2.3. Dynamics of laboratory populations of Collembola

As a first practical example, we used data from the monitoring of experimental populations of the Collembola *Folsomia candida*, a parthenogenetic ametabolous hexapod commonly used as a laboratory model organism in soil biology (Fountain & Hopkin 2005). The individuals were bred at 21°C in cylindrical plastic boxes of 5.3 cm diameter with a 3 cm thick plaster substrate to keep the environment damp (Tully & Ferrière 2008) (Fig. 1A). The studied populations were fed weekly with a mix of yeast in agar-agar in a fixed quantity and kept in the dark the whole time. Measures of the number and size of individuals (Fig. 1B) were taken every one or two weeks during about 600 days (~ 85 weeks) using image analysis (Mallard et al. 2013).

2.4. Dynamics of a wild population of woodlice

As another applied example, we used the data from a published follow-up of the seasonal dynamic of the structure of a population of the woodlouse *Armadillidium vulgare* (Hassall & Dangerfield 1990). We extracted from the original figure (a succession of head width pyramids, see Fig. 4A) the percentage of the population within each class of head width for each date.

2.5. Package STdiag usage

To easily display the dynamics of a structured population, we developed the package `STdiag`, which is freely available at R-forge (R-forge.r-project.org) and can be installed in R with the following command:

```
install.packages("STdiag",
dependencies = TRUE, repos = c
("http://R-Forge.R-project.org",
"http://cran.cnr.berkeley.edu"),
type = "source")
```

The package can then be loaded using the command `library(STdiag)`.

2.6. Importing and formatting the data

Data frame. `STdiag` uses the `lattice` function `levelplot` (Sarkar 2008) as the core plotting function. As a consequence, the basic data format is a three column data frame containing the X (time), Y (structure such as age or size) and Z (number of individuals) coordinates. The data frame has $T \times S$ lines where T is the number of time values and S the number of structure classes.

Matrix. Another possibility is to use a matrix description of the data using two vectors x and y of size T and S , respectively, for the time and structure coordinates, and a matrix z of size $T \times S$ containing the number of individuals at each coordinate. This mimics the format used in the base function `image` (The R Development Core Team 2012). In case one wishes to convert data from a matrix to a frame format, the function `Matrix2DataFrame` is provided and it can be used, for instance, as follows:

```
time = c(1:100); structure =
c(1:10); count = matrix(data =
runif(10*100, min = 0, max = 200),
nrow = 100, ncol = 10) # random data
DataFrame <- Matrix2DataFrame(count,
time, structure, xlab = "time",
ylab = "structure", zlab = "number")
# conversion
```

Individual based data. The function `Indiv2DataFrame` is also provided to convert individually based data to a data-frame that can be plotted with `STdiag`. The package comes with `IndivData`, a table with more than 110,000 individual body length measurements of springtails in a population tracked during about 1.5 years. The `Indiv2DataFrame` handles a data-frame containing one line per individual and, in columns for each individual, the time of the observation and the value of the structuring element (body length in our example). The option `classes` allows to control the number of classes in which the structure variable is discretised. A single value produces the desired number of regular classes (default set to 50), whereas a vector specifies the breaks of the classes as in the base function `hist`. This function is used as follows:

```
data(IndivData) # to load the data
DataFrame <- Indiv2DataFrame
(IndivData, classes = 50)
or
DataFrame <- Indiv2DataFrame
(IndivData, classes = seq(0,10,0.1))
```

2.7. Generating the plots

Data frame. The simplest way to generate the basic plot is to use the data frame formulation. If the columns of the data frame are in a time-structure-number order, a simple call to `STdiag (DataFrame)` will produce the plot. If one wants to specify what columns to plot, the function `STdiag` accepts the formula syntax:

```
STdiag(counts~date*size,
data = DataFrame)
```

In any of those or the following forms, the vector used as time can either be a numeric vector or a vector of dates of classes `POSIXlt`, `POSIXct` or `Date`. Class factor is not yet supported for date format.

Matrix. We provide `matrixSample`, a matrix with demographic springtail data as a practical example. To use the matrix formulation, one can either call `STdiag(matrixSample)`, in which case X and Y-axes will be default vectors from 1 to T and S , respectively, or, if one wants to specify the x and y coordinates, using the `time`, `structure` and `count` objects created above:

```
STdiag(x = time, y = structure,
z = count).
```

2.8. Improving the graphical representation

Our method is implemented with several options to adjust the plot to be as informative as possible.

Colour palette. The readability of the diagram partly relies on the choice of colours for the palette (Fig. 2A, B). The hues are sorted following either a grey scale from pale grey to black or an adapted rainbow gradient (Fig. 2A, B, C). This can be adjusted using the option `color = "palette"` inside `STdiag()`, where `palette` can be one of the following: `gray`, `topo`, `terrain`, `heat`, `cm`, `rainbow` or by default `tim` [see `tim.colors` in library `fields` (Furrer et al. 2012)]. One can also use the package `RColorBrewer` or the function `colorRampPalette` from the package `grdevices` to create custom palettes. In Fig. 4B we have used the `RColorBrewer` palette with nine different colours. The command to generate Fig. 4 is:

```
STdiag(PercentOfTotal ~ Date *
HeadWidth, data = woodlice,
color = list('custom', brewer.pal(9,
'YlOrBr')), log = T, main = "Woodlice
population", ylab = "Head width, mm",
xlab = "Date")
```

The option `color = list('custom', brewer.pal(9, "YlOrBr"))` creates a colour palette which is not the default one (hence the keyword `custom`). We use the `brewer.pal` palette from the `RColorBrewer` package, which provides some nice looking colour palettes especially for thematic maps. 9 is the number of different colours used and `"YlOrBr"` is one of the diverging sequential palettes provided by the `RColorBrewer` package. Refer to the `?brewer.pal` for more detailed information.

Logarithmic scale. When the number of individuals in the different classes differs by several orders of magnitude (Fig. 1B), we recommend using a logarithmic scale for the Z-axis to increase the readability of the generated graphics. Using the option `log = FALSE` or `log = TRUE` allows the user to switch easily between linear and logarithmic colour scales.

Interpolation. The quality of the diagram can sometimes be improved by applying an interpolation to smooth the representation and link together uneven time intervals by creating evenly spaced data (Fig. 2D). The interpolation method creates an artificial dataset with evenly distributed data, based on the original data. It is essential to make a clear distinction when reading such a diagram between the real data and data created by the interpolation and we recommend to first use a non-interpolated representation of the data. To interpolate the data, we provide the function `Interpolation` in the package. This function is an interface to the function `interp.surface` in package `fields` adapted to quickly handle data in the format accepted by the function `STdiag`. It takes as an argument the data frame to be interpolated in the form of three columns: time, structure

and number of individuals, in that order. The options `intervX` and `intervY` allow the user to manually choose the intervals between two interpolated points, respectively over X (time) and Y (structure) axes. If those options are left empty, the function uses the minimum distance between two points in the first and second columns as intervals for X and Y-axes, respectively.

Kernel density estimate. The function `STdiag` provides an option `smooth = TRUE` to plot a weighted kernel density estimate of the data using an axis-aligned bivariate normal kernel, where the data are the time-structure coordinates weighted by the number of individuals. The estimate is derived from the function `kde2d` in package `MASS` (Venables & Ripley 2002). The density estimate can be adjusted with options `sm`, a positive scalar (0 meaning the original data and 1 being the normal reference distribution kernel estimation bandwidth) defining the smoothness of the kernel density estimate, and `n`, the number of points on the X Y grid. Together, these options allow viewing a smooth representation of the structured data (Fig. 2E, F). Contrary to the interpolation, the kernel density estimate only provides a smooth representation of the data. In the case of missing data, such as irregular time intervals, interpolating the data before plotting the kernel density can avoid having gaps in the density for a low smoothing factor (small `sm`).

Code. The code used to generate Fig. 2 is given in the following lines. We used the data 'sample' which is provided in the library `STdiag`, so these lines can be executed directly after loading the package.

```
data(sample)
st1 = STdiag(z~x*y, data = sample,
xlab = "Time", ylab = "Structure",
color = "gray", main = "Gray
Palette")
st2 = STdiag(z~x*y, data = sample,
xlab = "Time", ylab = "Structure",
color = "tim", main = "Tim Palette")
st3 = STdiag(z~x*y, data = sample,
xlab = "Time", ylab = "Structure",
color = "tim", main = "Log Color
Scale", log = TRUE)
st4 = STdiag(z~x*y,
data = Interpolation(sample),
xlab = "Time", ylab = "Structure",
color = "tim", main = "Interpolated
data", log = TRUE)
st5 = STdiag(z~x*y, data =
Interpolation(sample), xlab = "Time",
ylab = "Structure", color = "tim",
main = "sm = 0.2", log = T,
smooth = TRUE, sm = 0.2)
```

```
st6 = STdiag(z~x*y, data =
Interpolation(sample), xlab =
"Time", ylab = "Structure", color =
"tim", main = "sm = 0.6", log = T,
smooth = T, sm = 0.6)
pdf(file = "figSTdiag.pdf", width = 7,
height = 16*7/9); print(st1);
print(st2); print(st3) ; print(st4);
print(st5); print(st6); dev.off()
```

Note that, since `STdiag` is a wrapper around the `lattice` function `image.plot`, the plots can be saved in a variable and printed using the base function `print`.

2.9. Extracting quantitative measurements from the diagrams

The function `STdiag.measure` can be used to interact with the diagram and obtain some quantitative measurements from it. The general syntax is `STdiag.measure(stdiag, type = c("point", "line"))`. First, the plot to be interacted with needs to be saved in a variable on which the function `STdiag.measure` is applied. One can, for instance, apply this function on the object `st3` previously created to measure the growth rate of a cohort `STdiag.measure(st3, type = "line")`. When the function is called, it will wait for the user to identify via mouse clicks one or two points (depending on the option `type`) in the panel being drawn. If used with the option `type = "point"`, it returns the position of the point identified with a single mouse click. This can be useful, for example, when measuring the size at birth on a diagram (white arrows on Fig. 2B, try `STdiag.measure(st2, type = "point")`) or the average size of a group of adults (star on Fig. 2C). If used with the option `type = "line"`, one has to click twice on the diagram and the function returns the slope of the line defined by the two points along with the coordinates of the points. This can be used to measure the growth rate of a cohort directly on the graphs [line on Fig. 2C with `STdiag.measure(st3, type = "line")`, and Fig. 4B], or the secular change of the size of adults in a population (Fig. 3). Finally, the option `region = TRUE` provides the possibility of extracting a region of the plot, i.e. a subset of the data around the chosen point or line. With it, the option `range` can be used to adjust the window of selection. More precisely, `range` is a factor of the mean distance between two coordinates to define the region to extract. If the desired point coordinates are `x` and `y` and the original data are `data`, the region is defined by `x` in the interval `x-range*mean(diff(unique(data$x))), x+range*mean(diff(unique(data$x)))` and the same applies to `y`.

For example `STdiag.measure(st2, type = "point", region = TRUE, range = 3)` will provide the `x`, `y` and `z` values of the selected point together with the `x`, `y`, and `z` values of all the points in a region centred around the clicked point. This second piece of information can be used, for example, with the function `weighted.mean` to measure the mean body size of the individual in the region:

```
test = STdiag.measure(st2, type =
"point", region = TRUE, range = 3)
weighted.mean(test$region$y,
test$region$z)
```

Note that one has to avoid using a logarithmic scale (`st2`) when using the `weighted.mean` function to estimate the mean size of a group of individuals.

Of course, one has to bear in mind that these measurements rely on where one clicks on the graph. We advise users to be cautious about this, especially when the graphics are noisy. Measuring the repeatability may be useful at this stage in order to estimate the reliability of these measurements.

3. Results

3.1 Dynamics of springtail laboratory population

The structure-time diagrams of *Collembola* populations (Figs 2, 3) immediately reveal the predominance of the younger class (<0.5 mm). The populations are usually bimodal (juveniles and adults, Figs 2, 3B) and sometimes trimodal (small and large adults; Fig. 3A). The use of a logarithmic scale (Fig. 2C) reveals some inter-class dynamics undetectable when using classical representations: for example, between day 150 and day 300 a cohort of small individuals grows and changes into adults. This visual display allows one to estimate some demographic parameters that cannot be seen on classical representations (Fig. 1) using the function `STdiag.measure` described above: size at birth (~ 0.28 mm, by observing spikes of births, white arrows in Fig. 2B), median adult length (1.2 mm around day 50, black star in Fig. 2C), growth rate of a cohort of juveniles striving to be recruited in the population (0.22 mm/month, slope of the straight line in Fig. 2C). It is also possible to study the long-term temporal dynamics of adult body length. Depending on different conditions (intensity of competition, quantity of resource, temperature), the mean length of the adults in the population can remain stable (when competition is intense, Fig. 3B, line 3), increase (when more food

is given in the rearing boxes, Fig. 3A, line 1, Fig. 3B, line 4) or even decrease (when competition between two cohorts is too intense, Fig. 3A, line 2, or when the amount of food provided is reduced, Fig. 3B, line 5). The different population structures revealed in Figs 2 and 3 result from genetic factors (Mallard et al. 2015, the lineage used in Fig. 3 produces trimodal populations, which is not the case for the lineage of Fig. 2) and from changes in the environmental conditions (in Fig. 3B, the amount of food provided each week is increased and then decreased, whereas it is maintained constant in the other case studies). These graphics illustrate the remarkable ability that the springtails maintain during most of their lifespan to resume growth or even to shrink when the environmental conditions change.

3.2. Dynamics of a wild population of woodlice

Two different representations of the dynamics of a woodlouse population have been displayed in Fig. 4 as an example of a wild population of a soil organism. This original representation (Fig. 4A) already shows some cohort dynamics. Put side by side, the pyramids without accounting for the time that separates them makes it difficult to extract any valuable temporal information. The corresponding structure-time diagram (Fig. 4B) –with head-width as the structuring element– can be used to directly measure and compare the growth rates of the different cohorts. The representation is noisy due to a limited temporal and structural resolution, but one

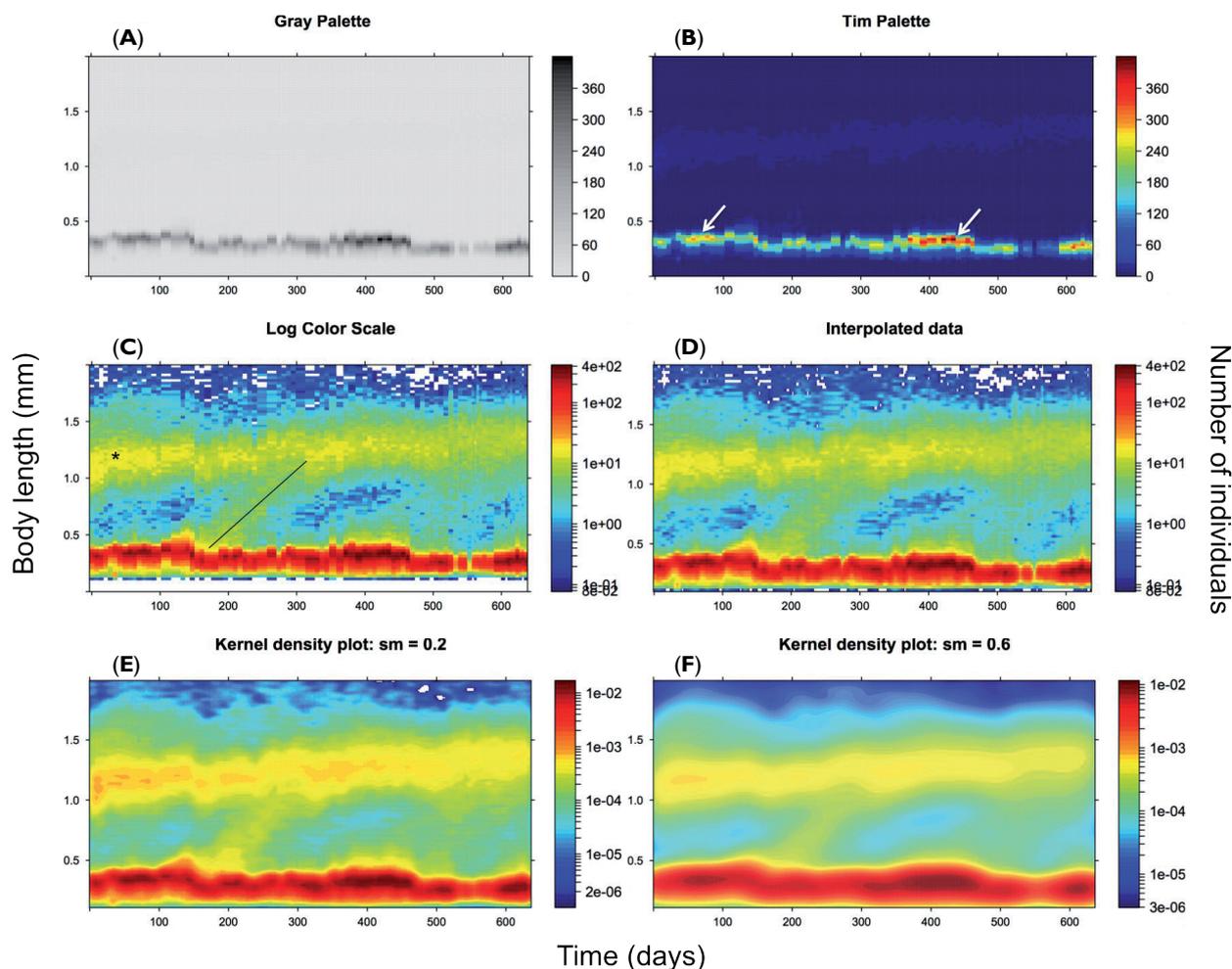


Figure 2. Collembolan population dynamics plotted with STdiag. Length is discretised into classes of 0.05 mm length. The number of individuals at each date length coordinate is represented on a linear grey (A) or colour (B) scale or on a logarithmic scale (C, D). Panel (D) represents an interpolated version of panel (C). Panels (E) and (F) represent two kernel density estimates with increasing smoothness. After using these smoothing methods, the meaning of the scale of the z-axis cannot be easily interpreted anymore. These smoothed representations may be useful to visually reveal an overall message from the data, while hiding some details and noise. On average, the population is mostly composed of small individuals (~ 0.4 mm) living with some adults (~ 1.2 mm). Logarithmic scale reveals details about the recruitment of some cohorts, the growth rate of which can be estimated (black line, C). See main text for details about the options used to produce the different plots.

can easily recognise the alternation of cohorts visible in Fig. 4A. This example demonstrates the applicability of structure-time diagram to even low resolution ecological data, and its generality in terms of type of data to represent.

4. Discussion

A multi-dimensional diagram such as our structure-time diagram (Fig. 2B) is preferred to a simple time series representation (Fig. 1C, D) for several reasons: time series representation lacks the continuity of the structuring element and, thus, even when time series plots represent different classes of individuals (Fig. 1D), the representation with lines makes it difficult to detect and analyse any cross class dynamics. A three-dimensional diagram offers a unique and complete visual display of the variations of the population structure and is thus a very powerful tool for the description of a population and a convenient way of guiding the analysis. We show that it can be used to track the details of the population dynamics of *Folsomia candida*, a lab-model species in ecotoxicology, and this approach could be used to study the effects of a pollutant on several components of the populations dynamics (fecundity, recruitment, cohorts growth rates, size and number of individuals etc.) and not only on the number of surviving individuals after a given time period, as is usually done. Moreover, by juxtaposing several structure-time diagrams, one can add an extra dimension to the graphical display, such as the

sex of the individuals or any other categorical variable (population, genotype, etc.). If one uses the same axis for these diagrams, one can compare at a glance the complex dynamics of several categories of individuals.

The structure-time diagram does not need individuals to be identified from one time to the other. And without any individual trajectories, changes in the structure over time directly draw dynamics of cohorts (as in Fig. 2C).

STdiag can also be used to represent any type of data with a structuring factor like age or size and an aggregate statistic such as mortality rate (Vaupel et al. 1987) or body mass (Ozgul et al. 2009). It can also be used for displaying data from a numerical model (Le Bourlot et al. 2014) or data from medical surveys or demographic studies to reveal any secular or seasonal changes for example.

Such diagrams fulfil the criteria for excellence in statistical graphics (Tufté 1990): they show many numbers within a small space (high data density), thus making large data sets coherent without distorting the data; they reveal the data at several levels of detail, from fine structure to broad overview; they encourage the eyes to compare different pieces of data and induce the viewer to think about the substance rather than about the method (Tufté 2001).

With the development of automatic data acquisition and prolific databases (Le Galliard et al. 2012, Mallard et al. 2012, 2013), the use of such a graphical display should become more common in population ecology, but also in many other fields such as human demography, epidemiology or medical surveys.

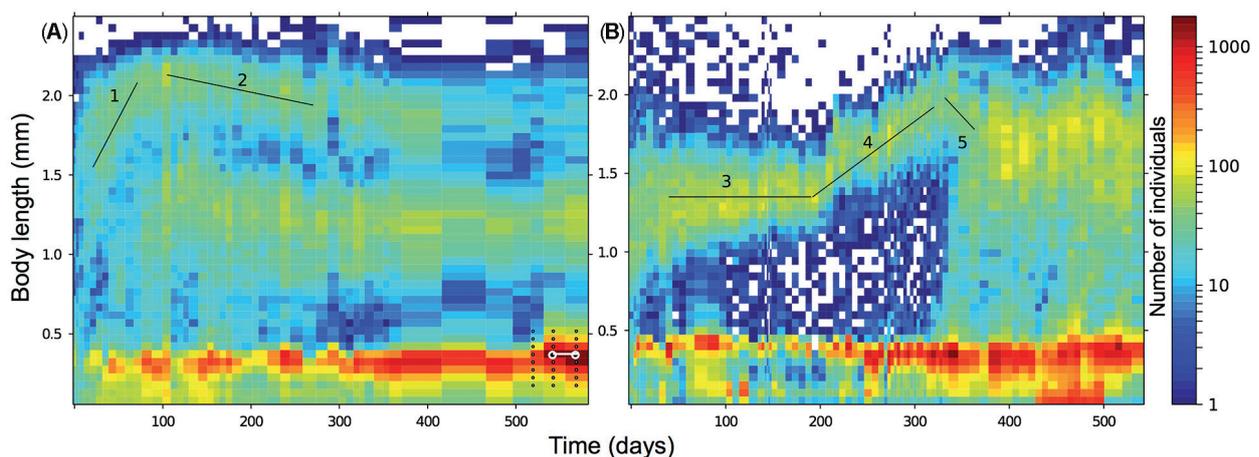


Figure 3. Two laboratory populations of springtails followed during 1.6 years. (A) Three cohorts of juveniles grow and recruit during the first 150 days. The second and third cohorts reach a smaller adult size than the first one. After about 200 days, the population structure reaches an almost stable trimodal distribution made of large and small adults and of juveniles that do not manage to grow anymore. This graphic also reveals that the mean size of the cohort of large adults shrink between about 100 and 300 days (line 2). (B) This diagram shows the remarkable plasticity of the cohort of adults, which can resume growth after more than 200 days when the amount of food provided has increased. It is only after about 340 days, when the adults have ceased growing, that the juveniles can benefit from the improved environmental conditions by growing themselves. These two graphs reveal the strong size-dependent interference competition, which is a primary factor driving the population structure dynamics in this system (Le Bourlot et al. 2014).

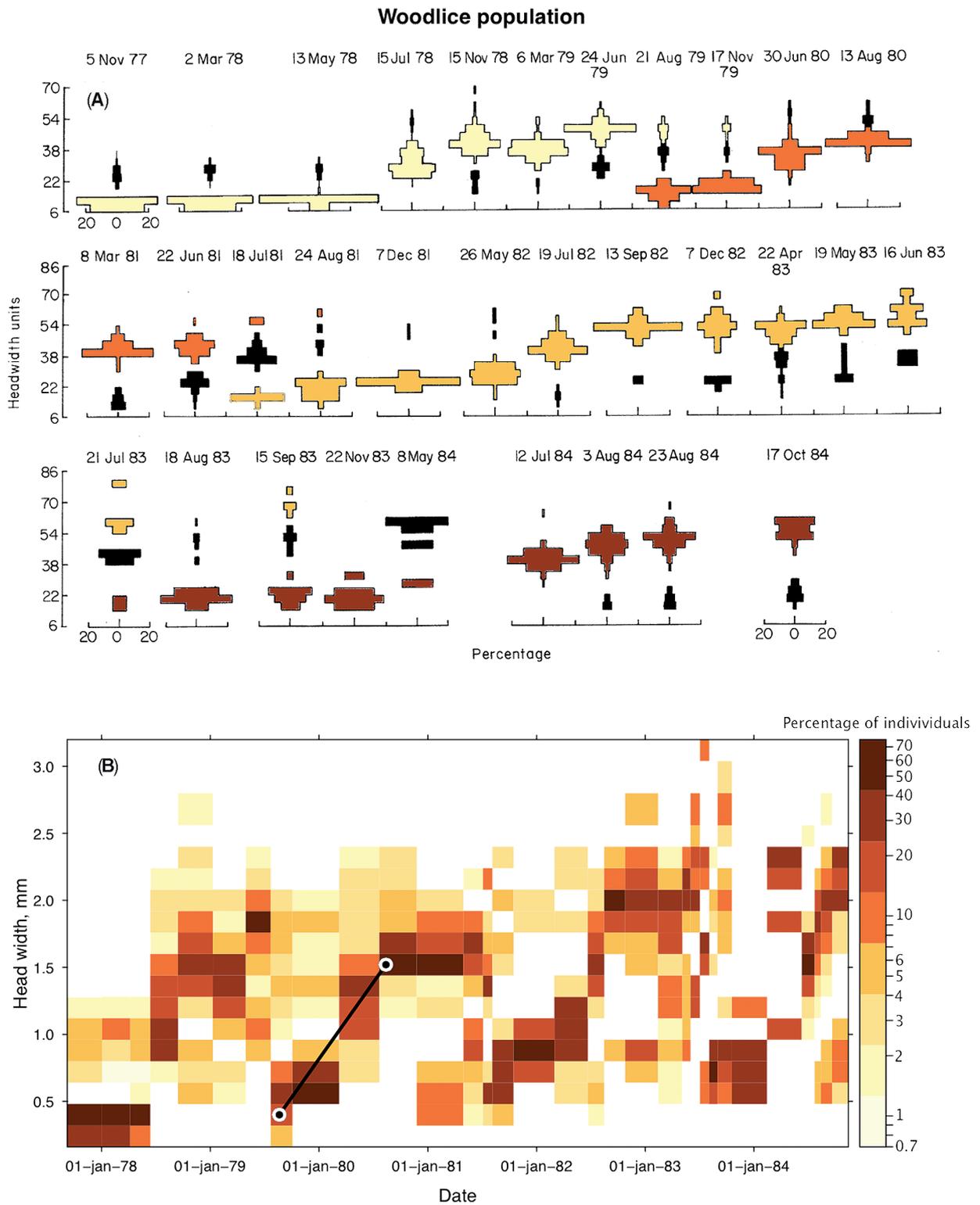


Figure 4. Dynamics of a woodlice population. **(A)** Original figure representing the seasonal variation of a woodlice population structure (expressed in %, one head unit = 0.04 mm, Hassall & Dangerfield 1990). Coloured boxes are individuals born in odd years, black boxes represent individuals born in even years. **(B)** Same data represented with a structure-time diagram. This diagram can be directly used to measure the growth rate of the different cohorts (1.14 mm/year for the cohort born in summer 1979).

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