PS Determining Percentage Carrying Capacity and Delayed Percentage-Dependency Lags in Palaeontological Time Series, Illustrated Using Benthonic Foraminifera in the Cipero Formation (*Catapsydrax Stainforthi* Zone, Lower Miocene) of Trinidad, Western Tropical Atlantic Ocean*

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Abstract

The percent carrying capacity K_p is the percentage of a species an area can support while meeting very individual's needs. It is determined from a time series of percentage abundances for species i, where p_{it} is the abundance of that species at time t. The percentage point change in abundance Δp_i between samples is given by $\Delta p_i = p_{it+1} – p_{it}$, where p_{it+1} is the percentage abundance at time (t + 1). The rate of change for each percent r_i is given by $r_t = \Delta p_i / p_{it}$.

Linear regression of r_t against p_{it} gives $r_t = r_m – s \bullet p_{it}$, where r_m is the rate of increase in r_t as p_{it} approaches zero, and the slope s shows the strength of intraspecific, interspecific and abiotic interactions for the species investigated. Setting $r_t = 0$, $p_{it} = K_p$ and $r_m – s \bullet K_p = 0$, which gives $K_p = r_m/s$. Nonlinear regression gives $r_t = r_m – s \bullet \ln(p_{it})$, from which $K_p = \exp(r_m / s)$. Delayed percentage-dependency lags (DPDLs) are determined by plotting phase portraits of r_t vs. p_{it} at lags (t + 2), (t + 3) . . . (t + x) and examining the regressions' goodness of fit.

Nonlinear regressions showed better goodness of fit than linear regressions for abundant species in the Lower Miocene Cipero Formation of Trinidad. Values of r_m and s show that *Gyroidinoides* cf. *soldanii* was the most opportunistic species of those examined and *Pullenia bulloides* the least. Species showed different DPDLs, *Stilostomella nuttalli gracillima* and *Cibicidoides mundulus* showing a best fit at (t + 1), *Pleurostomella cubensis* and *Globocassidulina subglobosa* at (t + 2), *Nuttallides umbonifera* at (t + 3), and *G*. cf. *soldanii*, *Oridorsalis umbonatus* and *P*. *bulloides* at (t + 4). The range of DPDLs argues against simple abiotic control by, say, glacial-interglacial cycles.

Determining percentage carrying capacity and delayed percentage-dependency lags in paleontological time series, illustrated using benthonic foraminifera in the Cipero Formation (*Catapsydrax stainforthi* Zone, Lower Miocene) of Trinidad, western tropical Atlantic Ocean

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Introduction and theoretical background

Ecologists collect time series of species' abundance data and from them determine carrying capacities, maximum reproduction rates and the strength of intraspecific and interspecific competition. Simple modifications allow these measures to be applied to time series of percentage abundance data of fossils.

This poster thus uses statistics. Please accept my apologies for that.

The percent carrying capacity K_p is the percentage of a species an area can support while meeting very individual's needs. It is determined from a time series of percentage abundances for species *i*, where p_{it} is the abundance of that species at time *t*. The percentage point change in abundance $d(p_{ij})$ between samples is given by $d(p_{ij}) = (p_{it}+1) - p_{it}$, where $(p_{it}+1)$ is the percentage abundance at time (t+1). The rate of change for each percent r_t is given by $r_t = d(p_t)\ /p_{it}$.

Linear regression of r_t against p_{it} gives $r_t = r_m - s{\cdot}p_{it}$, where r_m is the rate of increase in r_t as p_{it} approaches zero, and the slope *s* shows the strength of intraspecific, interspecific and abiotic interactions for the species investigated. Setting $r_t = 0$, $p_{it} = K_p$ and $r_m - s{\cdot}K_p = 0$, which gives $K_p = rm/s$. Nonlinear regression gives $r_t = r_m - s{\cdot}\ln(p_{it})$, from which $K_p = \exp(r_m / s)$.

Populations may exhibit cyclical, longer-term behavior than at a lag of (*t*+1) due to lethargic (time delayed) but possibly density dependent processes. Such populations show delayed percentage-dependent lags (DPDLs) that are determined by plotting phase portraits of r_t vs. p_{it} at lags (*t* + 2), (*t* + 3) . . . (*t* + x) and examining the regressions' goodness of fit. See Figure 1.

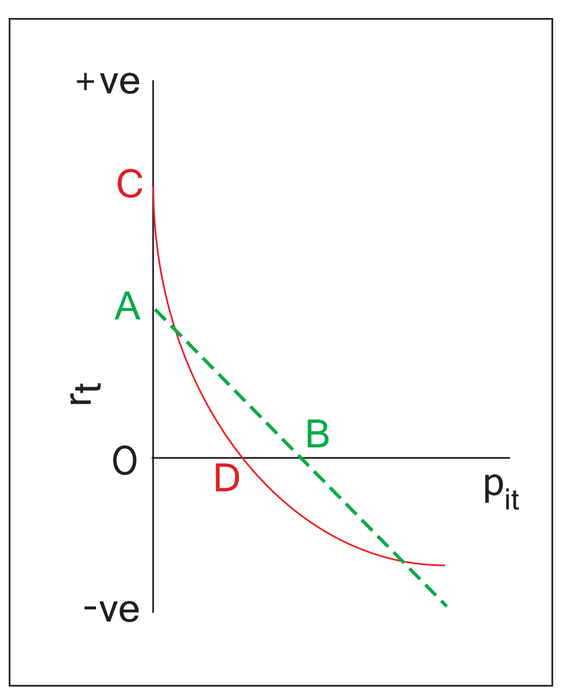

FIGURE 1. Interpreting linear and nonlinear regression of a phase portrait in which:
– p_{it} = percentage of assemblage comprising species *i* at time *t*
– r_t = percentage rate of increase per percent for p_{it}
– Straight, dashed line = linear regression
– Curved, solid line = nonlinear regression.
– A = r_m, value of r_t as p_{it} approaches 0 for linear regression
– B = percent carrying capacity K_p for linear regression
– C= r_m for nonlinear regression
– D = K_p for nonlinear regression

Method

The data are from Wilson (2008) for the Lower Miocene Cipero Formation (*Catapsydrax stainforthi* planktonic foraminiferal Zone) exposed by roadworks south of a roundabout midway between San Fernando and Cross Crossing (GR0670730/1133505, Figure 2). Samples JBW-194 through JBW-223 were taken where possible at 5 m intervals, with a mean spacing of ~5.5 m. Wilson (2008) picked 6506 benthonic foraminifera in 192 species from the 29 samples. Values of p_{it} for each species in each sample were calculated.Analyses were conducted using abundant and consistently occurring species (each >5% of total recovery):

- *Cibicidoides mundulus* (6.1%),
- *Gyroidinoides* cf. *soldanii* (5.2%),
- *Oridorsalis umbonatus* (8.6%)
- *Siphonodosaria nuttalli gracillima* (6.5%).

Linear ($r_t = r_m - s{\cdot}p_{it}$) and nonlinear ($r_t = r_m - s{\cdot}\ln(p_{it})$) regressions were conducted on the phase portraits of r_t versus p_{it}. The percent carrying capacity K_p was determined from either $K_p = r_m / s$ or $K_p = \exp(r_m / s)$, depending on whether the linear or nonlinear model respectively showed the better fit.

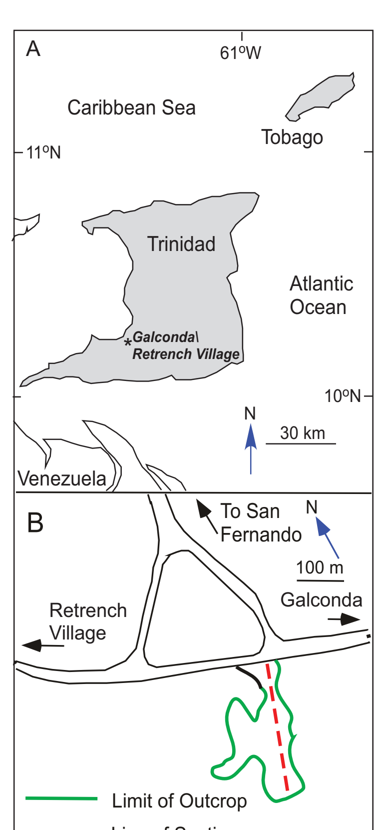

FIGURE 2.

Species	Order	Linear regression	*r*	*p*	K_p
Cibicoides mundulus	*t* + 1 (~5.5 m)	$r_t = 2.572 - 0.272p_{it}$	-0.5	0.02	9.5
Gyroidinoides cf. soldanii	*t* + 4 (~22 m)	$r_t = 2.531 - 0.324p_{it}$	-0.6	0	7.8
Oridorsalis umbonatus	*t* + 4 (~22 m)	$r_t = 1.696 - 0.144p_{it}$	-0.6	0	11.8
Siphonodosaria nuttalli gracillima	*t* + 1 (~5.5 m)	$r_t = 2.86 - 0.132p_{it}$	-0.3	0.07	–
Species	**Order**	**Nonlinear regression**	***r***	***p***	K_p
Cibicoides mundulus	*t* + 1 (~5.5 m)	$r_t = 4.498 - 2.274\ln(p_{it})$	-0.6	0	7.2
Gyroidinoides cf. soldanii	*t* + 4 (~22 m)	$r_t = 4.821 - 2.599\ln(p_{it})$	-0.8	0	6.4
Oridorsalis umbonatus	*t* + 4 (~22 m)	$r_t = 3.667 - 1.575\ln(p_{it})$	-0.7	0	10.3
Siphonodosaria nuttalli gracillima	*t* + 1 (~5.5 m)	$r_t = 4.09 - 1.79\ln(p_{it})$	-0.6	0	9.8

TABLE 1. Linear and nonlinear regressions of phase portraits of selected species in the Lower Miocene Cipero Formation of Trinidad. The column 'order' indicates any delayed percentage dependence lag DPDL, while K_p is the percentage carrying capacity calculated for the phase portrait for the DPDL with the best fit.

Results

See Table 1 and Figure 3.

Siphonodosaria nuttalli gracillima showed a toothed time series (Figure 3A) not suggestive of long-term cyclicity. This is confirmed by the first order phase portrait of rt against pit (Figure 3B). Linear regression at a lag of (t + 1) returned a statistically insignificant result. Non-linear regression at (t + 1) gave a better, significant fit. Thus, this species showed nonlinear pattern of first order dynamics in p_{it}.

Cibicidoides mundulus had a toothed time series (Figure 3C, D). Linear regression gave the statistically significant expression $r_t = 2.5724 - 0.2722p_{it}$ (r = –0.45, p = 0.02). Substituting into $K_p = r_m / s$ gives a K_p of 9.6%. However, a better fit overall was obtained using nonlinear regression, which shows that *C. mundulus*, like *S. nuttalli gracillima*, had a nonlinear pattern of first order dynamics in p_{it}.

Gyroidinoides cf. *soldanii* had a time series of more-or-less smooth peaks and troughs suggestive of a percentage dependent lag (Figure 3E, F). First order nonlinear regression gives a better, statistically more significant fit than does linear regression. However, the best fit was from nonlinear regression at (t + 4), suggesting that a negative feedback acts on the *G.* cf. *soldanii* population at a delay of the time indicated by four samples or ~22 m.

Oridorsalis umbonatus had a time series positively and significantly correlated (r = 0.442, p = 0.016) with that of *G.* cf. *soldanii.* Nonlinear regression analysis shows a DPDL at (t + 4) (~22 m).

Discussion and conclusions

Wilson (2012) used the linear regression $r_t = r_m - s{\cdot}p_{it}$ to model percent carrying capacities K_p in the Upper Quaternary of the Santaren Channel. In the Cipero Formation, nonlinear regression in the form $r_t = r_m - s{\cdot}\ln(p_{it})$ provides a better fit.

The value of r_m reflects a species' ability while at low values of p_{it} to make headway towards dominance. Species with high values may show more opportunistic behavior than those with low values. In the Cipero Formation, the values of r_m for nonlinear regressions were highest for *G.* cf. *soldanii*.

The negative slope *s* of the nonlinear regression represents the severity of the impacts of interspecific and abiotic factors. The steeper the slope, the less challenging the environment for the species. In the Cipero Formation, the environment was least challenging for *G.* cf. *soldanii*. Values of K_p varied between species, being greatest for *O. umbonatus*.

DPDLs, instead of showing the interactions of predators and prey detected by ecologists, in paleoecological time series can potentially determine the impact of long-term abiotic factors (intensity of upwelling, bottomcurrents, glacial-interglacial cycles) on species' abundance. However, in the Cipero Formation, species show first through fourth order phase portraits. The factors determining these differing delayed percentage-dependent lags have yet to be determined.

Oridoralis umbonatus

Gyroidinoides cf. *soldanii*

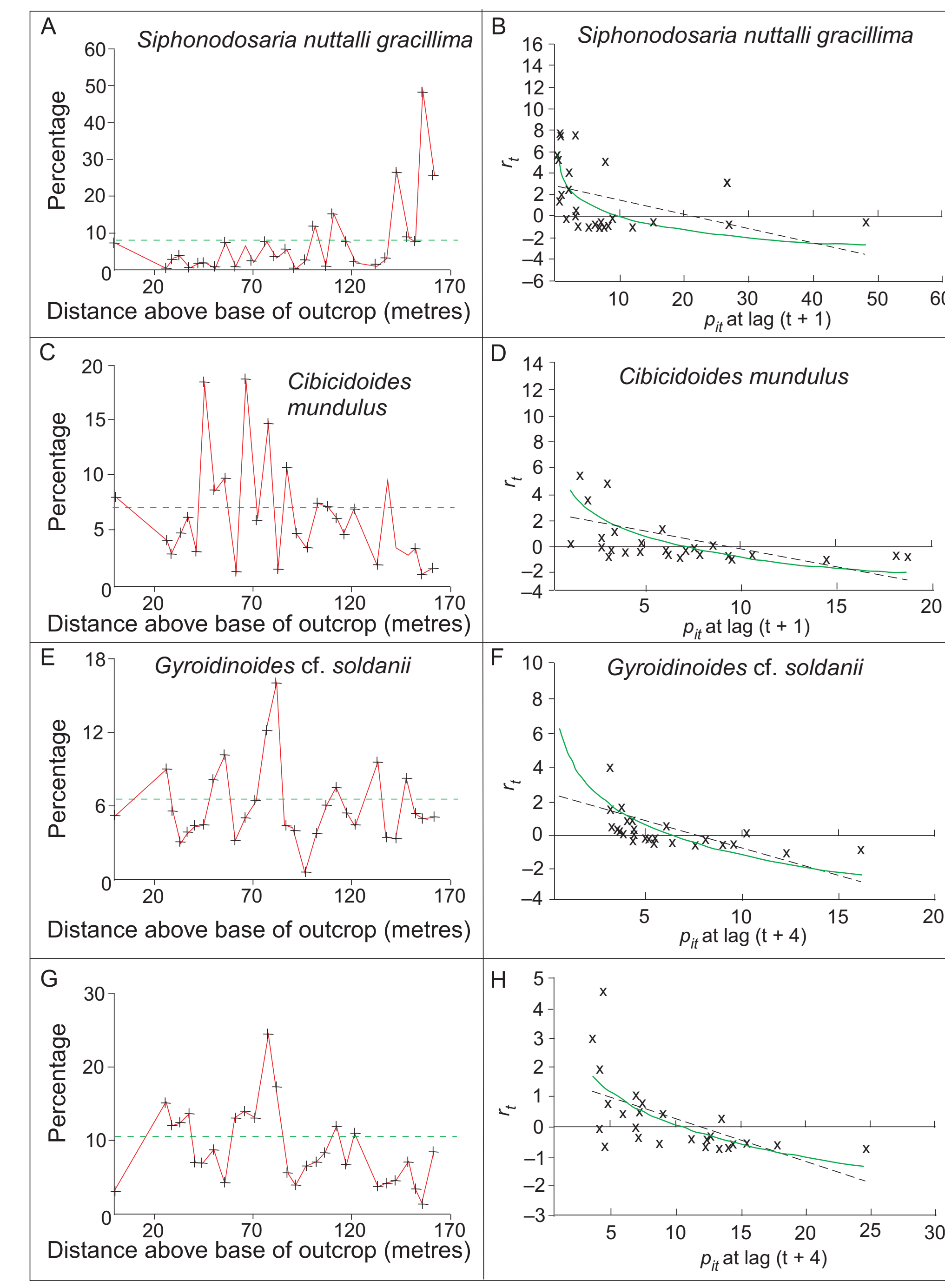

FIGURE 3. Time series (base of studied section at left) and phase portraits for species in the Cipero Formation of Trinidad. Inter-sample vectors in the phase portraits have been omitted for clarity. Horizontal dashed lines in A, C, E and G are percentage carrying capacities. Dashed line in phase portraits B, D, F and H are linear regressions, while solid lines are nonlinear regressions.
– A, time series for *Siphonodosaria nuttalli gracillima.*
– B, phase portrait for A at a lag of (t + 1).
– C, time series for *Cibicidoides mundulus*.
– D, phase portrait for C at a lag of (t + 1).
– E, time series for *Gyroidinoides* cf. *soldanii*.
– F, phase portrait for E showing delayed percentage-dependency lag at (t + 4).
– G, time series for *Oridorsalis umbonatus.*
– H, phase portrait for G showing delayed percentage-dependency lag at (t + 4).

Acknowledgments

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