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Assessment of assemblage-wide temporal niche segregation using null models

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Summary

1. Although time can be subdivided to promote species coexistence, quantitative examination of assemblage-wide temporal niche overlap has seldom been explored with appropriate null models. Because of the sequential and continuous nature of time, it requires a different kind of randomization model than those used to assess subdivision of discrete and non-sequential resources (e.g. food types and microhabitats).

2. For two common niche overlap indices (Pianka and Czekanowski), we compared the responses of two common randomization models and a newly developed model (ROSARIO) to different levels of temporal autocorrelation, specialization and coincidence of activity.

3. Although qualitatively similar results characterized overlap indices, results differed depending on randomization model. Temporal resolution of the data and amount of temporal specialization in an assemblage can have large effects on model outcomes. ROSARIO is as powerful as the models used for analyses of overlap of nominal and unordered resources, but it is more appropriate for ranked and interval data, as it maintains the empirical temporal autocorrelation within species.

4. ROSARIO can be a useful tool for exploration of assemblage-wide patterns of overlap in the use of resources that occur as cyclical phenomena, such as diel phases, yearly seasons, lunar tides and climate oscillations.

Key-words: activity patterns, chronobiology, community structure, cyclical phenomena, Monte Carlo simulations, niche overlap, temporal niche partitioning

Introduction

A major goal of ecology is to understand the bases for species coexistence in local communities (Weiher & Keddy 1999). The three primary mechanisms that facilitate coexistence involve interspecific subdivision of food, space or time (Schoener 1974a). Although seldom explored from an empirical perspective, temporal partitioning is considered to be uncommon (Schoener 1974b). Partitioning of larger time periods (i.e. seasons or years) may be a consequence of correlated differences in resource dynamics (Loreau 1992), whereas partitioning of smaller time periods (i.e. diel) more likely involve interference competition (Carothers & Jaksic 1984). Other explanations for diel patterns include the interplay of predation and historical (i.e. phylogenetic) factors that affect foraging (Kotler, Brown, & Hasson 1991; Kronfeld-Schor & Dayan 2003; Fraser *et al.* 2004). In a temporally partitioned community, each species should be able to obtain exclusive access to space or food, facilitating coexistence and enhancing local richness.

Temporal separation can occur at several scales. Some coexisting species reduce overlap by using different seasons (Loreau 1985, 1989). Alternatively, differences in activity between night and day facilitate coexistence of species (e.g. nectarivorous birds during day vs. nectarivorous bats at night; see Arrington & Winemiller 2003). Nonetheless, evidence for interspecific differences in activity patterns within higher taxa that are diurnal (e.g. among nectarivorous birds) or that are nocturnal (e.g. among nectarivorous bats) have not been explored in a comprehensive fashion, with only a few exceptions (e.g. pairs of desert rodents, Kronfeld-Schor & Dayan 1999; Jones, Mandelik, & Dayan 2001; Gutman & Dayan 2005). Although experimental studies that involve pairs of species provide insights into the mechanisms that promote temporal segregation of activity, the feasibility of using such an approach in

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species-rich communities in structurally complex environs (e.g. tropical forests) is quite limited as the number of pairwise combinations [$S(S-1)/2$] increases rapidly with richness (S). Moreover, such experiments only detect pairwise interactions, not assemblage-wide patterns of temporal overlap. In natural assemblages (*sensu* Fauth *et al.* 1996), all species potentially vie for resources, thus creating simultaneous interactions that should be addressed at the assemblage level. Null models using a summary index can be effectively used to discern patterns at the assemblage level. This analytical tool compares observed index values to a distribution of comparable values from assemblages that are constituted in the absence of a particular mechanism (Gotelli & Graves 1996).

Time as a resource has some characteristics that distinguish it from other niche axes. For example, time in the diel context is a sequentially ordered and continuous resource, in that 24-h cycles of day and night are continuous, with the last hour of night (e.g. 05·00–06·00 h) followed by the first hour of the day (e.g. 06·00–07·00 h). Such a sequentially ordered and continuous resource requires a different kind of randomization model than those used to analyse the subdivision of resources that are not sequential, such as food or microhabitat types (Winemiller & Pianka 1990). In spite of the clear arguments provided against the use of models intended for non-sequential resources to analyse time overlap (Gotelli & Graves 1996), examples persist in the literature that use those models (Prieto & Danhers 2009) potentially providing erroneous results. Simulation models that assess non-ordered resources reshuffle data among all possible resource states (Winemiller & Pianka 1990). Consequently, when applied to a time cycle, they remove temporal autocorrelation, as they destroy the shape and location of activity, creating an overly large null space, including biologically unfeasible possibilities (i.e. species with disjointed patterns of activity). Incorporation of critical properties of data structure into null models is fundamental to developing tests that provide ecologically meaningful answers (see Harms *et al.* 2001). As such, an alternative approach involves random shifts of entire activity patterns within a relevant time extent (i.e. time period containing all activity for the assemblage). This approach has been used to address temporal overlap of activity among species at seasonal (Fleming & Patridge 1984; Tokeshi 1986; Loreau 1989) and diel cycles (Castro-Arellano *et al.* 2009; Presley *et al.* 2009). Such a simulation framework preserves the temporal structure of the activity for each species but varies its location within the time extent. An overarching assumption of continuous models is that the form of activity patterns has been moulded strongly by natural selection (Kronfeld-Schor *et al.* 2001), but that its location is constrained by agonistic interactions (Carothers & Jaksic 1984), physiological constraints (DeCoursey 2004) or resource limitations (Loreau 1992). Thus, continuous models presume that they test the evolutionary strategy of activity of each species as constrained in the assemblage by abiotic and biotic conditions particular to it. Although this model fits better the criteria set forth for analyses of time overlap (Gotelli & Graves 1996) compared with randomization models devoted to sequential resources (Winemiller & Pianka 1990), the quantitative results from both approaches have never been contrasted systematically. In this context, we explored the performance of three randomization models as a tool for evaluating assemblage-wide temporal niche overlap. Specifically, we tested these models with respect to different levels of temporal resolution or temporal specialization of species.

Materials and methods

SIMULATION FRAMEWORK

Our proposed method analyses species (rows)-by-time (columns) matrices that are populated with frequencies of occurrence (e.g. captures and detections). The Monte Carlo approach that we develop requires a measure of temporal niche overlap between pairs of species ($\alpha_{j,k}$). For this purpose, we used the Pianka (Pianka 1973) and Czekanowski indices (Feinsinger, Spears, & Poole 1981) because they are common measures of overlap in resource use. Each index is symmetric, approaches zero for species that have non-overlapping activity patterns, and equals 1·0 for species that have identical activity patterns. The proportional use of time i by species j and k is p_{ij} and p_{ik} respectively. If n time intervals are recognized, Pianka's index of overlap is calculated as:

$$\alpha_{j,k} = \frac{\sum_{i=1}^{n} p_{ij}p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^{2}p_{ik}^{2}}} \qquad \text{eqn 1}$$

Alternatively,the Czekanowski index of overlap is calculated as:

$$\alpha_{j,k} = 1{\cdot}0 - 0{\cdot}5\Big(\sum_{i=1}^{n} |p_{ij} - p_{ik}|\Big) \qquad \text{eqn 2}$$

[Correction added after online publication 3 August 2010: eqn 2 corrected].

To quantify temporal niche segregation at the assemblage level, we calculated the mean of the overlap index derived from all possible pairwise comparisons [$S(S-1)/2$] of species in the assemblage. We determined the significance of niche segregation by comparing the empirical mean to a frequency distribution of such metrics derived from simulated assemblages for which temporal patterns of species were randomized (i.e. pseudo-assemblages; Pianka 1973). If species interactions or preferences for abiotic conditions drive partitioning of time (i.e. segregated activity patterns), empirical metrics should be among the smallest of simulated values. Conversely, an unusually large metric (i.e. coincident activity patterns) points to shared resource use or abiotic constraints on activity (e.g. temperature). For all tests, we used 10 000 iterations to generate null distributions, and considered significance at $\alpha = 0{\cdot}05$. The empirical data required to populate the species-by-time matrix should be an accurate representation of time use by each species. To address diel overlap, for example, a single day of observations will not be adequate as diel patterns can be affected by numerous phenomena that can vary greatly among days. Independent observations should be collected over several days until the activity pattern of each species is more or less invariant to additional sampling.

Three different models were employed to generate null distributions of assemblage-wide temporal overlap. All of them have been used to address temporal overlap (Albrecht & Gotelli 2001; Castro-Arellano *et al.* 2009; Prieto & Danhers 2009). We used random algorithm 3 (RA3) and random algorithm 4 (RA4), both implemented by EcoSim (Winemiller & Pianka 1990; Gotelli & Entsminger 2006), as well as a new model (ROSARIO) modified from those described by Fleming & Patridge (1984), Loreau (1989) and Tokeshi (1986).

We named this new model ROSARIO, after the tradition of rosary praying in which beads are advanced in a circular fashion (analogous to the progression of time).

In RA3, all entries for each species (row) are randomized, allowing use of any of the time intervals in the time extent. Species maintain the amount of specialization (i.e. number of zero states or time intervals with no activity), but temporal autocorrelation is destroyed. In RA4, empirical zero states are fixed, and only non-zero entries are randomized so that simulated species maintain levels of specialization equal to that of the empirical species. RA4 is relatively conservative compared with RA3, with RA4 being more subject to type II error relative to RA3 (Winemiller & Pianka 1990). If the time utilization matrix has no zeros, results from RA3 and RA4 will be the same, as their only difference is how each model treats zeros in a matrix.

In ROSARIO, much of the empirical autocorrelation in activity for each species is maintained because only the continuous distribution of activity patterns is shifted over time. More specifically, we generated a series of alternative activity patterns for each species by advancing the empirical pattern in sequence until its peak (modal activity) occupied each of *n* time intervals that make up the time extent. Each alternative distribution (*n* is the number of time segments in the extent) represents exactly the same activity distribution but with a different location within the time extent. Additionally, we included *m* distributions that are mirror images of each one of the previously created distributions. The suite of 2*n* distributions represents a complete set of possibilities (Fig. 1). Previous models (see Tokeshi 1986; Loreau 1989) did not include mirror image distributions, and as such had incomplete null spaces in random simulations. In each iteration of ROSARIO, a pseudo-assemblage is formed by randomly selecting one of these possibilities from each of the 2*n* distributions of each of *S* species. As time-of-day is 'circular', we permitted activity patterns to wrap around the time extent (Fig. 2). If activity encompassed a full diel cycle, it is satisfactory to let distributions move freely throughout the day. However, inclusion of all time intervals (i.e. 24 h) in tests of temporal overlap for either nocturnal or diurnal organisms is undesirable, as the simulations will always discern species' use of time as aggregated (i.e. avoiding night or avoiding day). Consequently, for overlap analysis within a time extent (e.g. night), ROSARIO restricts distributions to be within these time periods (Fig. 2, from interval F to D for a nocturnal time extent). ROSARIO is implemented by the TimeOverlap program that runs in the Windows operating system. The program is available from the authors on request or can be downloaded from http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity%20pattern.html together with an example data file and a supplemental text file that describe the use of the TimeOverlap program.

DESCRIPTION OF CONSTRUCTED EXAMPLE DATA SETS

To facilitate assessment of model performance, we created two sets of constructed examples. A first set of 12 examples evaluated the interaction between temporal resolution and temporal overlap, whereas a

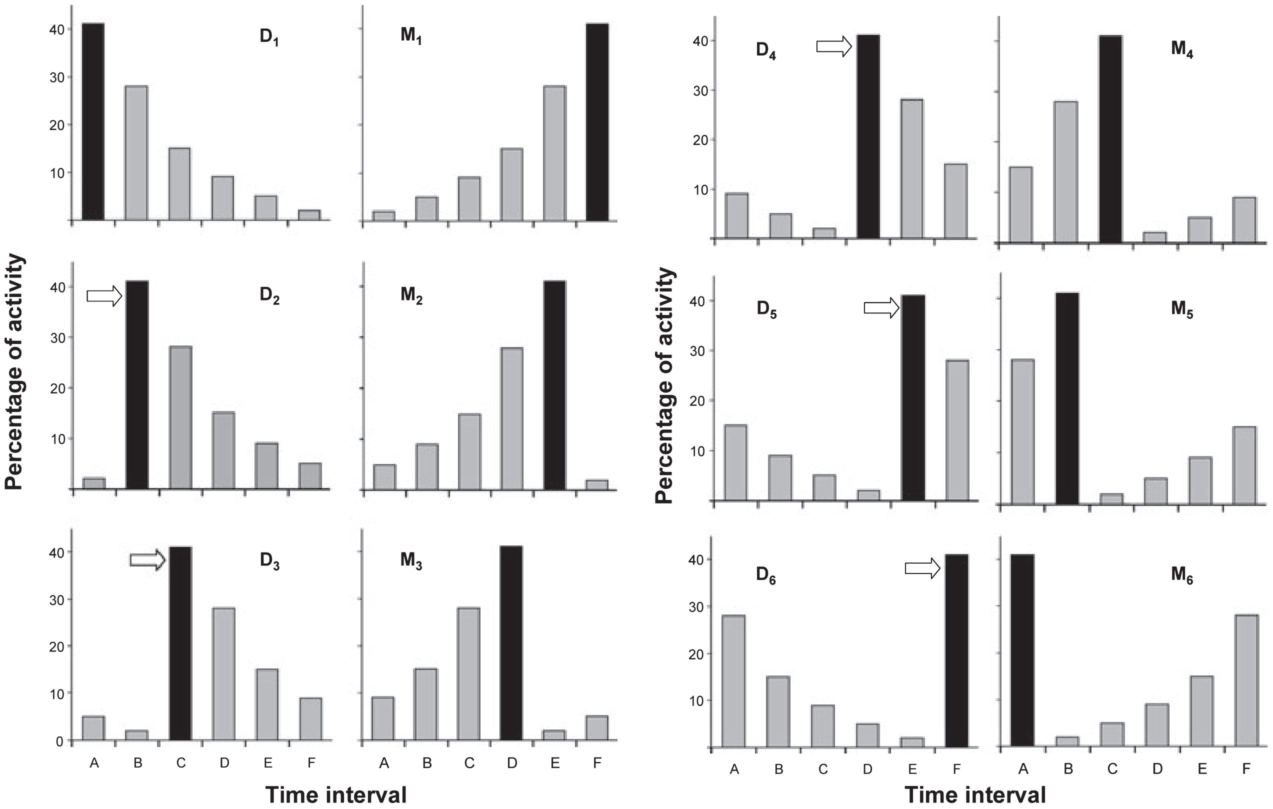

Fig. 1. Diagrammatic illustration of the basis of ROSARIO model. A hypothetical temporal activity pattern of a species over a domain is divided into $n = 6$ intervals as portrayed in plot D_1. The left column (plots D_1–D_6) displays all possible options obtained by incrementally advancing the original pattern over the time domain. The right column (plots M_1–M_6) represents mirror images that correspond to the patterns on the left. The suite of 2*n* distributions represents a complete set of possibilities in which the empirical mean, variance and temporal structure of the data are maintained, but the position of the curve changes along the domain. In each iteration, one of these options is selected at random to form part of the pseudo-assemblage. For complete details of simulations, see text.

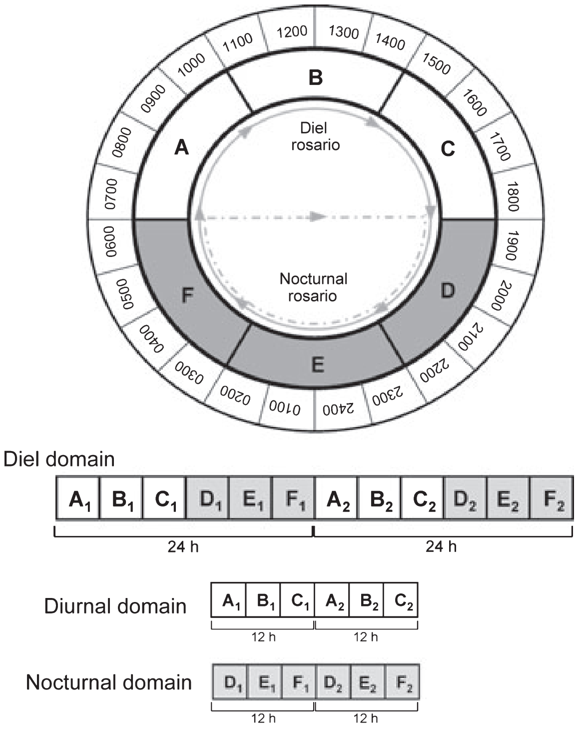

Fig. 2. Diagrammatic illustration of how the ROSARIO model 'wraps' distributions of activity along examples of diel, diurnal and nocturnal time extents. In this example, six intervals (A–F) compose the full diel extent. For analysis done at a diel extent, the movement of distributions would be from F to A (solid grey arrows); for a nocturnal extent, the movement would be from F to D (stippled grey arrows); and for a diurnal extent, the movement would be from C to A.

second set of 25 examples examined the interaction between temporal specialization of species and temporal overlap. Examples used to assess temporal resolution had five species with similar empirical patterns of activity arranged in three cases: coincident modal activities (i.e. peaks of the activity distributions), modal activities distributed at random or maximally segregated modes. A random number generator was used to assign the location of modal activities for each species in the random assemblages. To evaluate effects of temporal resolution on significance, we used a progression of 6, 12, 24 and 48 intervals to sample these assemblages (Fig. 3). We calculated temporal autocorrelation based on a time lag of one time unit for the activity pattern of each species, and derived an average temporal autocorrelation for each level of temporal resolution.

To assess the effect of specialization and overlap, we created matrices of 12 time intervals in which five species had similar activity patterns (Fig. 4). We varied the amount of specialization, producing examples with high (three intervals with non-zero activity), medium (six intervals with non-zero activity) or low specialization (all intervals with activity). For each level of specialization, we evaluated a progression of overlaps that ranged from coincident modes, to modes separated by one time step, to modes separated by two time steps, to random allocation of modes and to modes separated into two groups of two and three species (Fig. 4). Finally, to evaluate the presence of zeros, we substituted all inactive intervals with low levels of activity (0·1%), for examples with low and medium temporal specialization. As the main goal of this second set of examples was to compare ROSARIO with the other models, we used a replicated simulation approach to compare the average *P*-value of 100 tests with ROSARIO against the equivalent *P*-values obtained with RA3 or RA4.

To evaluate model efficacy with respect to particular patterns of specialization or overlap, we used artificial data sets (rather than empirical data) to avoid intrinsic idiosyncrasies (e.g. habitat heterogeneity and weather changes). However, application of the ROSARIO model to real data sets can be found in comparisons of bat temporal activities between forest and disturbed areas (Castro-Arellano *et al.* 2009; Presley *et al.* 2009) and in the assessment of temporal segregation of subtropical rodent communities (Castro-Arellano & Lacher 2009). Each study provides detailed ecological background for the test of temporal overlap within the context of empirically documented assemblages.

Results

As qualitative results for each index were similar, we present only the results for the Czekanowski index. When patterns are strong, all models were generally able to detect significance (Fig. 3, Table 1). However, ROSARIO was not affected by changes in the temporal autocorrelation for simulated scenarios, whereas RA3 and RA4 generally provided more liberal *P*-values given the larger null spaces they create (Fig. 3, random mode examples). All models were able to detect extreme overlap as a non-random pattern regardless of temporal specialization or inclusion of zeros (Fig. 4, top row, coincident mode examples).

In most cases, ROSARIO provided quantitatively different results when compared with RA3 and RA4 (in 80% and 84% of cases respectively; Table 1). In the vast majority of results that differed quantitatively, a bias existed towards lower *P*-values for RA3 (19 of 20 cases) and RA4 (16 or 21 cases) when compared with ROSARIO. The few cases for which ROSARIO had smaller *P*-values were mostly for RA4 when zeroes were prevalent in the data matrix (i.e. RA4 for both one- and two-step segregated modes, Table 1). Nevertheless, these numerical differences do not always translate into different levels of significance (e.g. all cases with randomly located modes; Table 1). In almost half (RA3, 8 of 20) and a third (RA4, 6 of 21) of the comparisons where there were differences between ROSARIO and the other indices, ROSARIO had higher *P*-values that translated to a different significance level (i.e. non-significant vs. significant). In all these cases, RA3 and RA4 were more liberal and designated significant temporal overlap patterns, whereas ROSARIO was more conservative and indicated patterns with overlap not different from random expectation. For most (22 of 25) of the examples, differences between RA3 and RA4 were small (Table 1). Differences between these two models only appeared at intermediate levels of temporal specialization. Substitution of zeros by minimal levels of activity did not affect outcome for any models. Similarly, differences between the outcomes of RA4 and RA3 are minor for matrices where there are no zeros.

Discussion

Statistical significance from the Rosario simulations corresponded to the degree of temporal overlap in constructed examples. For example, our model detected either strong

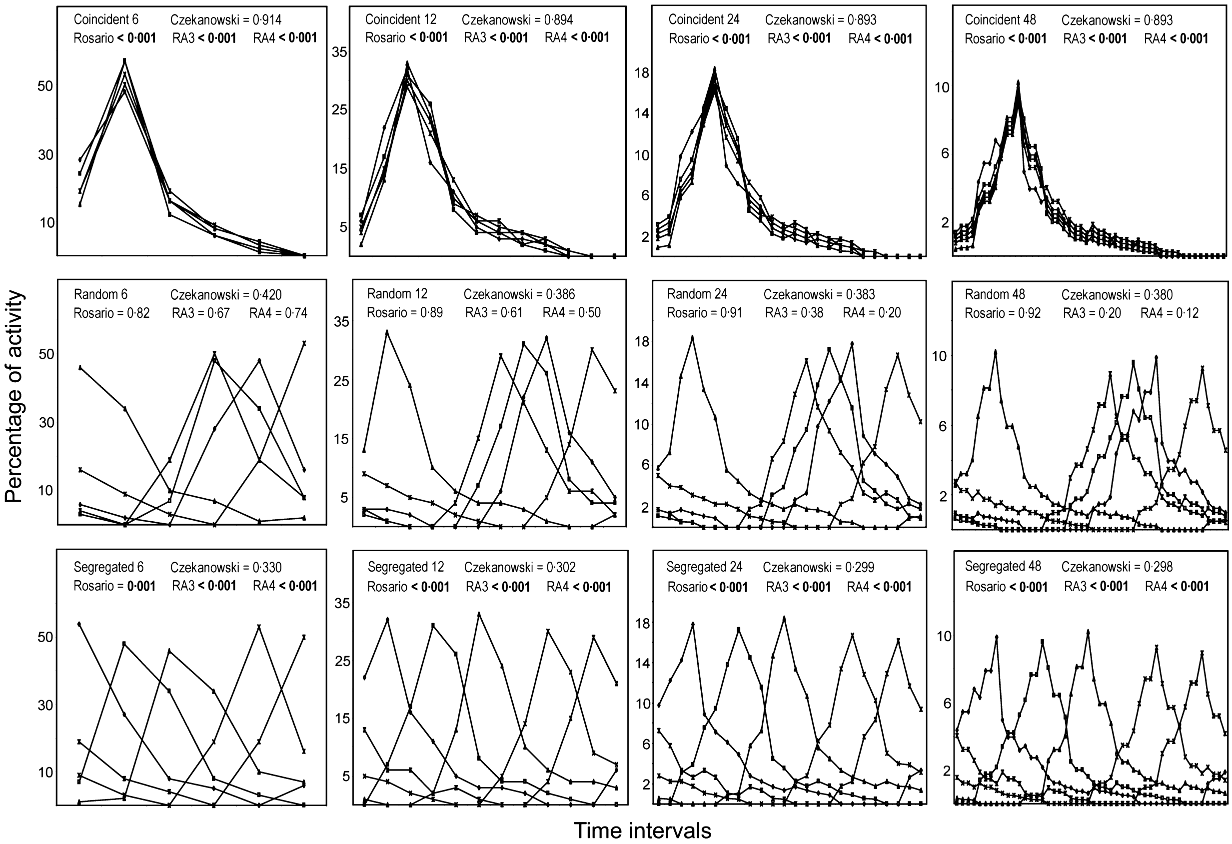

Fig. 3. Response of RA3, RA4 and ROSARIO to levels of temporal autocorrelation and subdivision of the time extent with respect to three cases: (1) coincident modes (top row), (2) random location of modes (middle row) and (3) segregated modes (bottom row). Columns correspond to a progression of temporal resolution from 6 to 48 intervals, with a matching average temporal autocorrelation of 0·257, 0·663, 0·867, 0·938. *P*-values for each model (RA3, RA4 and ROSARIO) are two-tailed probabilities of obtaining deviations as large as or larger than those in the empirical community by chance alone. Czekanowski values correspond to the observed overlap measured with Czekanowski index.

patterns of coincident activities or strong patterns of segregated activities in situations constructed to display each situation. Similarly, all models yielded non-significance for examples with random distribution of activities. However, the models evinced different sensitivities to intermediate scenarios. Several related factors can potentially affect the ability to detect temporal overlap: temporal resolution of the data (number of intervals that compose a time extent), degree of temporal specialization of each species (i.e. number of time intervals with zero activity), temporal autocorrelation of activity of the constituent species and number of species in an assemblage.

Analysis of temporal overlap in a diverse assemblage is a complex endeavour because of several sources of variation (Loreau 1989). Activity patterns of particular species could follow any of three idealized activity patterns: unimodal, bimodal or constant. Moreover, noise is inherently present in any collection procedure of activity data (Halle & Stenseth 2000), leading to reduced power.

Given this complexity, the challenge is to develop a null model that shuffles only one source of variation, while maintaining all other factors constant (Gotelli & Graves 1996). In the case of temporal niche overlap, ROSARIO is a better model compared with either RA3 or RA4 for methodological reasons, and should be the preferred method for analysis of assemblage-wide temporal overlap. Sequential as opposed to unordered resource states require different null models for testing patterns of assemblage-wide overlap. RA3 and RA4 were devised for nominal unordered resources (e.g. categories of prey or microhabitat) where their arrangement is irrelevant (Winemiller & Pianka 1990). As such, they provide an answer for a different hypothesis of resource use. By contrast, time categories are interval data in which position along a niche axis is important. As ROSARIO maintains the order of the data, it is a better model based on first principles and provides a more ecologically reasonable perspective (see Harms *et al.* 2001). ROSARIO generates variation in randomized simulations related only to overlap, as it does not disrupt the shape of activities but only changes overall location. By contrast, RA3 and RA4 generate additional sources of variation in the randomization, other than those for which statistical inference is focused. Whenever ROSARIO indicates significance, it can only be attributed to overlap, whereas in RA3 and RA4, significance could be a consequence of the differences in temporal autocorrelation between empirical and simulated activity patterns. This distinction between models is reflected in the size of the null spaces that they create, with ROSARIO creating smaller null spaces. The advantage of ROSARIO is evident whenever high temporal autocorrelation within species and

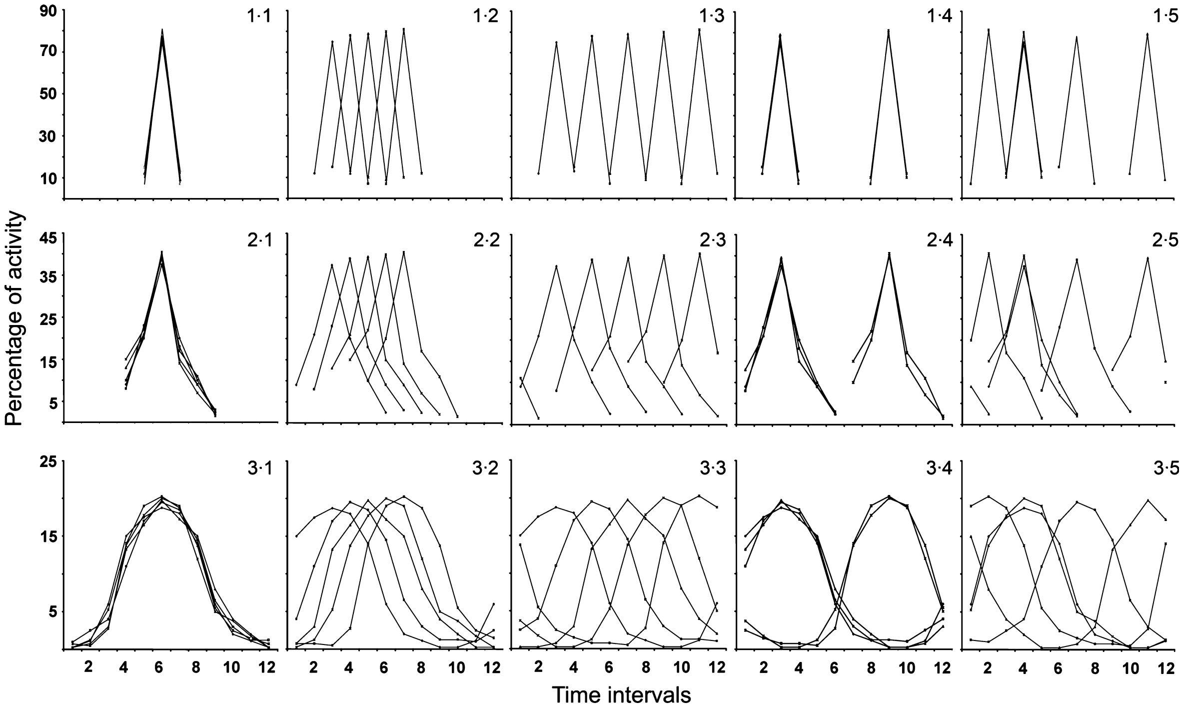

Fig. 4. Diagrammatic representations of constructed examples used to assess temporal overlap. Specialization changes from high (top row) to low (bottom row). Temporal overlap varies along each row from coincident modes, to modes separated by one time step, to modes segregated by two time steps, to two groups of modes and to random modes. Test results for all constructed examples appear in Table 1.

high temporal resolution, or both, are present. In these cases, RA3 and RA4 create large and unrealistic null spaces and are unduly liberal.

All the models that we tested assume that temporal niche breadths are constrained and have been fixed by natural selection. Allocation of activity within either diurnal or nocturnal phases has strong phylogenetic constraints (Roll, Dayan, & Kronfeld-Schor 2006) and physiological adaptations may limit the plasticity of activity patterns (Kronfeld-Schor & Dayan 2003). ROSARIO goes a step further and assumes that the shape of the activity pattern has been fixed, and only randomizes its location. Nonetheless, the performance of Rosario was only evaluated for assemblages of moderate size ($S = 5$). A fuller evaluation of the efficacy of the Rosario algorithm for detecting community-wide niche segregation in more species-rich assemblages is complex and an area ripe for future research. Comparison of models was unaffected by choice of overlap index as we obtained qualitatively similar results from both indices. Nevertheless, these indexes have different accuracy depending on ranges of resource overlap (Linton, Davies, & Wrona 1981).

ROSARIO is a useful tool for pattern exploration of assemblage-wide overlap of sequentially ordered resources organized as a cyclical phenomenon. For the present study our arguments centred on diel extents, but our modelling approach is time-scale independent and can be applied to scales larger than a day (e.g. annual and seasonal). As input to the TimeOverlap program is a species-by-interval matrix, no modifications are necessary. By varying the number and size of the intervals used to build the matrix, the analysis can be applied to any number of scenarios where different temporal resolutions and time extents can be addressed. Specifically, this model can be used to address resource use overlap along lunar and tidal cycles (Godefroid, Hosftaetter, & Spach 1998), yearly or seasonal cycles (Espirito-Santo *et al.* 2009), and climatic fluctuations such as the El Niño (Holmgren *et al.* 2001) and Milankovitch oscillations (Dynesius & Jansson 2000).

Null model analysis of temporal overlap does not provide a complete picture about temporally coincident or segregated assemblages. From a methodological perspective it is critical to recall that the model does not focus on particular pairwise overlaps. It instead examines assemblage-wide (i.e. cumulative) overlap that could conceal significant segregation between particular species. Moreover, it does not identify the mechanistic bases for the patterns but is an important step towards understanding the role of time as a basis for niche partitioning (Gotelli & Graves 1996). Our understanding of how time mediates ecological interactions and influences the structure of assemblages is still poor (Kronfeld-Schor & Dayan 2003). Even though temporal partitioning on a diel basis has been predicted to be rare on theoretical grounds (Schoener 1974b), it is impossible to assess the prevalence of such partitioning based on a few empirical assessments (Kronfeld-Schor & Dayan 2003). Our modelling approach is an advancement in several aspects: it provides a comprehensive and accurate assessment of the concept initially introduced by Loreau (1989); it uses a comprehensive model that includes mirror images of distributions in the construction of null spaces; and it incorporates the well-established approach of using averages of pairwise overlaps to address assemblage-level patterns

Table 1. Results of three different null model analyses of temporal niche overlap in constructed example matrices using Czekanowski overlap index

Type of constructed example	Fig. 4 Panel	TS	NZ	Observed Overlap	ROSARIO			RA3			RA4		
					P_{ave}	2SD	T	P	T	π	P	T	π
Coincident modes	1, 1	H	45	0·953	**< 0·001**	0·000	**R**	**< 0·001**	**R**	0·99	**0·020**	**R**	**< 0·01**
	2, 1	M	30	0·941	**< 0·001**	0·000	**R**	**< 0·001**	**R**	0·99	**< 0·001**	**R**	0·99
	3, 1	L	0	0·938	**< 0·001**	0·000	**R**	**< 0·001**	**R**	0·99	**< 0·001**	**R**	0·99
	na	H	0	0·956	**< 0·001**	0·000	**R**	**< 0·001**	**R**	0·99	**< 0·001**	**R**	0·99
	na	M	0	0·941	**< 0·001**	0·000	**R**	**< 0·001**	**R**	0·99	**< 0·001**	**R**	0·99
One-step separated modes	1, 2	H	45	0·109	0·808	0·021		0·760		**< 0·01**	0·160		**< 0·01**
	2, 2	M	30	0·433	0·172	0·011		**0·022**	**R**	**< 0·01**	0·518		**< 0·01**
	3, 2	L	0	0·633	0·149	0·011		**< 0·001**	**R**	**< 0·01**	**0·002**	**R**	**< 0·01**
	na	H	0	0·117	0·792	0·020		0·720		**< 0·01**	0·732		**< 0·01**
	na	M	0	0·437	0·173	0·012		**0·018**	**R**	**< 0·01**	**0·030**	**R**	**< 0·01**
Two-step separated modes	1, 3	H	45	0·036	0·084	0·007		**0·016**	**L**	**< 0·01**	0·268		**< 0·01**
	2, 3	M	30	0·205	0·069	0·007		**0·002**	**L**	**< 0·01**	0·060		**0·01**
	3, 3	L	0	0·431	0·114	0·010		**< 0·001**	**L**	**< 0·01**	**0·002**	**L**	**< 0·01**
	na	H	0	0·046	0·077	0·007		**0·014**	**L**	**< 0·01**	**0·018**	**L**	**< 0·01**
	na	M	0	0·212	0·066	0·006		**0·002**	**L**	**< 0·01**	**< 0·001**	**L**	**< 0·01**
Two groups of modes	1, 4	H	45	0·384	**0·019**	0·004	**R**	**0·008**	**R**	**< 0·01**	**0·048**	**R**	**< 0·01**
	2, 4	M	30	0·377	0·340	0·013		0·140		**< 0·01**	**< 0·001**	**R**	**< 0·01**
	3, 4	L	0	0·505	0·818	0·018		0·960		**< 0·01**	0·960		**< 0·01**
	na	H	0	0·392	**0·017**	0·003	**R**	**0·010**	**R**	**< 0·01**	**0·008**	**R**	**< 0·01**
	na	M	0	0·384	0·332	0·014		0·150		**< 0·01**	0·114		**< 0·01**
Random modes	1, 5	H	45	0·117	0·901	0·020		0·820		**< 0·01**	0·760		**< 0·01**
	2, 5	M	30	0·251	0·611	0·018		0·200		**< 0·01**	0·290		**< 0·01**
	3, 5	L	0	0·472	0·769	0·029		0·250		**< 0·01**	0·276		**< 0·01**
	na	H	0	0·126	0·895	0·018		0·860		**0·01**	0·840		**< 0·01**
	na	M	0	0·258	0·610	0·020		0·200		**< 0·01**	0·250		**< 0·01**

P-values for each algorithm (RA3, RA4 and ROSARIO) are two-tailed probabilities of finding non-random community-wide niche overlap. For ROSARIO, the average (P_{ave}) and corresponding two standard deviations (2 SD) of 100 analyses are shown. π is the probability that the *P*-values of RA3 and RA4 fall within the 99% confidence interval for ROSARIO (P_{ave}). All significant results are in bold. Tail (T) indicates whether the observed index occurs in the left-hand (L) or right-hand (R) tail of the simulated distribution. Values in the extreme right tail indicate coincident activity patterns, whereas values located in the extreme left tail indicate segregated activity patterns. For all cases, number of species was five and number of intervals dividing each time domain was 12. NZ, number of zeroes in the matrix; TS, temporal specialization; H, high; M, medium; L, low. A corresponding chart for most examples is indicated by its panel position in Fig. 4.

(Gotelli & Graves 1996). In addition, we make available a freely downloadable computer program for use by the ecological community (see the Materials and methods section). A computer program that implements an analysis of niche overlap for non-ordered resources is already available (Gotelli & Entsminger 2006). Nevertheless, as argued before (Gotelli & Graves 1996) and shown here these models provide a different hypothesis of resource use not applicable to cyclical phenomena. Availability of a computer program that runs a null model analysis intended specifically for the overlap analysis of sequentially ordered resources will probably aid in preventing misuse of temporal overlap null model analysis (see Prieto & Danhers 2009).

Halle & Stenseth (2000) proposed merging approaches from ecology and chronobiology to establish the new field of chronoecology. Although the response of the scientific community has been weak, there is an increased recognition of time as a resource and how it can be a mediator of interactions in ecological communities (Kronfeld-Schor & Dayan 2003). Development of a reasonable model for assessing assemblage-wide overlap or segregation in use of time will hopefully further catalyse this nascent subdiscipline of ecology.

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