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Patterns of coexistence of two species of freshwater turtles are affected by spatial scale

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Abstract

Inferring biotic interactions from the examination of patterns of species occurrences has been a central tenet in community ecology, and it has recently gained interest in the context of single-species distribution modelling. However, understanding of how spatial extent and grain size affect such inferences remains elusive. For example, would inferences of biotic interactions from broad-scale patterns of coexistence provide a surrogate for patterns at finer spatial scales? In this paper we examine how the spatial and environmental association between two closely related species of freshwater turtles in the Iberian Peninsula is affected by the geographical extent and resolution of the analysis. Species coexistence was compared across spatial scales using five datasets at varying spatial extents and resolutions. Both similarities in the two species' use of space and in their responses to environmental variables were explored by means of regression analyses. We show that a positive association between the two species measured at broader scales can switch to a negative association at finer scales. We demonstrate that without examination of the effects of spatial scale when investigating biotic interactions using co-occurrence patterns observed at coarse resolutions, conclusions can be deeply misleading.

Zusammenfassung

In der Gemeinschaftsökologie ist ein zentraler Ansatz, biotische Interaktionen aus der Analyse von Verbreitungsmustern der Arten abzuleiten, und dieser hat in der letzten Zeit im Kontext der Modellierung von Verbreitungen einzelner Arten an Interesse gewonnen. Dennoch bleibt unklar, wie die räumliche Ausdehnung und die Korngröße solche Schlussfolgerungen beeinflussen. Könnten zum Beispiel Schlussfolgerungen zu biotischen Interaktionen aufgrund von Mustern der Koexistenz auf einer höheren Skala als Ersatz für die Muster auf einer kleinräumigen Skala dienen? In dieser Veröffentlichung untersuchen wir, wie die räumlichen und umweltbezogenen Assoziationen zwischen zwei nahe verwandten Arten von Süßwasserschildkröten auf der iberischen Halbinsel durch die räumliche Ausdehnung und die Auflösung der Untersuchung beeinflusst werden.

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Durch die Auswertung von fünf Datensätzen mit unterschiedlichen räumlichen Ausdehnungen und Auflösungen wurde die Koexistenz der Arten auf verschiedenen räumlichen Skalen verglichen. Sowohl die Gemeinsamkeiten in der Raumnutzung der beiden Arten als auch ihre Reaktionen auf Umweltvariablen wurden mithilfe von Regressionsanalysen untersucht. Wir zeigen, dass eine positive Assoziation zwischen den beiden Arten gemessen auf einer großen Skala zu einer negativen Assoziation auf feineren Skalen werden kann. Wir demonstrieren, dass die Untersuchung von biotischen Interaktionen mithilfe von Mustern der Koexistenz bei grober Auflösung ohne die Berücksichtigung der Effekte der räumlichen Skala zu Schlussfolgerungen führen kann, die gründlich.

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Introduction

Several studies have attempted to infer biotic interactions from the analysis of spatial patterns using datasets compiled at the landscape or the species' geographical range scales (e.g., Anderson, Peterson, & Gómez-Laverde 2002; Bullock, Edwards, Carey, & Rose 2000; Mönkkönen, Forsman, & Thomson 2004; Sfenthourakis, Tzanatos, & Giokas 2005). Such analyses usually seek to infer the existence of competitive exclusion or competitive release from occurrence data, as predicted by the Volterra-Gause Principle (Hutchinson 1957). If two species show an extensive overlap in the use of resources and simultaneously show limited geographical overlap in their distributions, then the assumption is that competitive exclusion has an influential role governing their distributions (Abramsky & Sellah 1982; Gause 1934; Sfenthourakis et al. 2005). Geographical patterns coupled with niche modelling can also provide insights into the existence of competitive release if there is evidence that species occupy a wider range of niches in the absence of their competitor than in its presence (e.g., Anderson et al. 2002).

There are a number of uncertainties associated with analyses of spatial co-occurrence that must be taken into account. For example, several studies have demonstrated the scale-dependency of patterns and mechanisms of spatial coexistence (e.g. Firth & Crowe 2010; Snyder & Chesson 2004; Wiens 1989). Three mechanisms can drive patterns of coexistence among pairs of species - biotic interactions, habitat requirements, and historical factors, including dispersal limitation (Sfenthourakis et al. 2005) – and they can show different relative impacts at distinct spatial scales. For example, competition may produce negative co-occurrence patterns at finer scales, even if there is positive covariation between species occurrences at broader scales due to shared historical or climatic constraints (Firth & Crowe 2010; Wiens 1989). On the other hand, the demonstration that biotic interactions have spatial consequences becomes more difficult at broad spatial scales, since other factors such as spatial heterogeneity within the geographical unit may allow pairs of competing species to coexist (e.g. Araújo & Guisan 2006; Connor & Bowers 1987). Although it has often been claimed that competition or facilitation has a limited effect on species occurrences at broader geographical extents and coarser

resolutions (Bullock et al. 2000; Pearson & Dawson 2003), this inference still lacks robust quantitative testing (Guisan & Thuiller 2005; but see Araújo & Luoto 2007; Gotelli, Graves, & Rahbek 2010; Heikkinen, Luoto, Virkkala, & Pearson 2007; Soberón 2010). Furthermore, explicit discussion about the scales and aggregation levels to be considered in the study of large-scale ecological patterns is seldom found in most ecological research (Meyer, Jopp, Münkemüller, Reuter, & Schiffers 2010).

An additional source of uncertainty lies in the methodological limitations to testing for spatial association between species (Gotelli 2000). Species co-occurrences are often analysed using null-pattern-generating models, where a mechanism of interest is excluded (Sanderson 2000; Gotelli 2000). However the significance of the observed patterns greatly depends on the assumptions underlying the null models. Models of coexistence among species are particularly prone to type I errors, i.e., rejecting the null hypothesis when it is in fact true, in particular when observations show a strong spatial autocorrelation (Palmer & Van der Maarel 1995).

Here, we investigate patterns of co-occurrence between two native freshwater turtle species, the European pond turtle, Emys orbicularis (L., 1758), and the Mediterranean pond turtle, Mauremys leprosa (Schweigger, 1812), considering multiple spatial scales within the Iberian Peninsula. The geographical range of the two species overlaps widely in the Iberian Peninsula. In some regions of northern Iberia E. orbicularis extends its range beyond that of M. leprosa (Keller & Andreu 2002), while being absent from most of southeastern Spain where *M. leprosa* also occurs (da Silva 2002). Whilst E. orbicularis is distributed throughout Europe, M. leprosa is restricted to Iberia and North Africa. The wide zone of coexistence in the Iberian Peninsula can be partially explained by similarities between the historical constraints faced by the two populations, such as their retreat to similar glacial refuges and similar subsequent expansion patterns (Fritz, Barata, Busack, Fritzsch, & Castilho 2006).

Despite wide overlap in the geographic ranges of the two species, there is some empirical evidence that spatial segregation occurs between the two species at finer spatial scales. In Iberia, *E. orbicularis* is much rarer than *M. leprosa* and it is absent from many apparently favourable habitats (Segurado & Araújo 2004). At sites where the species co-occur, the



Fig. 1. The five datasets used in the analysis: (1) Iberian Peninsula, 50 km, (2) Iberian Peninsula, 10 km, (3) Portugal, habitat scale, (4) Southwestern coast, habitat, (5) Stream reach, microhabitat. Occupancy at the Iberian Peninsula at the 50-km scale is expressed as the percentage of occupied 10 km grid cells. Abundance at the microhabitat scale corresponds to the number of captures per day \times trap.

abundance of *E. orbicularis* is very low and tends to show a high predominance of adults (Segurado & Araújo 2008). Conversely, populations of *E. orbicularis* with balanced agestructures and abundances compared to those of *M. leprosa* were exclusively found in allotopic situations. This suggests that *M. leprosa* could be a limiting factor for the occurrence of *E. orbicularis* by means of competitive interaction.

This study provides an analysis of co-occurrence patterns between the two species. Specifically, we test the hypothesis that differences in the use of space between the two species become increasingly marked when moving from coarse to fine spatial resolutions. The test is accomplished by examining whether the two species have similar responses to environmental variables, using different sets of data taken from distinct extents and resolutions.

Materials and methods

Data

Distribution data for *E. orbicularis* and *M. leprosa* were compiled from five different datasets, varying in spatial extent, spatial resolution, and information content (Fig. 1). Detailed information on each dataset is listed in Table 1. The two broader-scale datasets include information for the whole

Iberian Peninsula and are based on the UTM grid system considering two resolutions: 50-km and 10-km. At 50-km resolution, species' data equalled the number of occupied 10km grid squares. Only 10×10 -km grid cells with no turtle records but with at least twenty recorded species according to the Spanish atlas of amphibians and reptiles (Pleguezuelos, Márquez, & Lizana 2002), were considered as confirmed absences. Absence data for Portugal were restricted to cells that were sampled by the first author. Only those 50×50 -km cells containing more than ten adequately surveyed 10×10 km cells were considered for the analysis. The third dataset included information on the presence/absence of species at 200-m river reaches surveyed throughout the Portuguese geographical range of *M. leprosa* (n = 217; see Segurado & Araújo 2004 for further details). The fourth dataset was based on preliminary results of an ongoing study in the Southwest Coast of Portugal (Segurado, unpublished data). The 30×30 km study area included part of a river basin and a coastal plain with scattered shallow temporary ponds. Environmental data were extracted according to various buffer sizes: 5-m radius buffers for local variables and 250-m radius buffers for landscape variables. The fifth dataset consists of relative abundance data and microhabitat variables measured at 25-m intervals along a 1.3-km Mediterranean stream reach. Microhabitat variables were extracted according to 5 m radius buffers. The stream is located within a geographical region of

Database ID	Spatial scale	Resolution	Species' data	Sample size	Environmental variables	Number of environmental variables
1	Geographical range	50 km grid cells (UTM)	Number of occupied 10 km grid cells	182	Climate ^e	14
5	Geographical range	10 km grid cells (UTM)	Presence/absence ^a	3655	Climate, ^e hydrology, land cover, ^f human population density ^g	30
3	Geographical range	200 m line transects	Presence/absence ^b	217	Habitat ^b	29
4	Regional $(30 \mathrm{km} \times 30 \mathrm{km})$	5–250 m radius buffer ^h	Presence/absence ^c	66	Land cover, ^g habitat, ^c microhabitat ^c	26
5	Local (1.2 km)	5 m radius buffer ^h	A bundance ^d	52	Microhabitat ^d	16
Sources of infor ^a Godinho et a ^b Segurado an	mation: 1. (1999), da Silva (2002), Keller <i>a</i> 4 Araújo (2004).	nd Andreu (2002) and the UNIF	3A database (www.cea.uevora.pt/u	mc).		

²Segurado (unpublished data).

¹Segurado and Figueiredo (2007).

^eNew, Hulme, and Jones (2000; see Segurado et al. (2006) for more detailed information).

^gGrid them with 2.5 min resolution (available at: http://www.diva-gis.org/data/DataServer.htm). ^cCorine Landcover 2000 data set (Bossard, Ferane, & Otahel 2000)

Circumference around each observation, corresponding to the resolution at which the environmental variables were recorded

(Segurado & Figueiredo 2007). Species sampling consisted mainly in the detection of basking individuals. For some locations - particularly those containing habitats with few available basking sites – and for the stream reach dataset, sampling consisted of trapping sessions using baited hoop nets. Forty-seven variables extracted

at several spatial scales were considered for the analyses, each dataset including a different combination of variables according to their relevance for each spatial scale (see Appendix A). Environmental variables at the 10 km and 50 km spatial resolutions were resampled at the same grid resolution as the species' occurrence data using average values for the continuous variables and class percentages for the land cover variables. Most of the information was processed and integrated in a GIS environment using ArcGis 9.1 (ESRI Inc., Redlands, CA, USA).

Southern Portugal where the two turtle species widely coexist

Data analysis

Species coexistence was investigated considering both similarities on the use of space (i.e. geographical coordinates) and similarities in the response to environmental variables. Spatial association was examined by testing the ability of one species to explain the occurrence or abundance of the other, using a regression approach. Since E. orbicularis occupies a broader environmental range within the Iberian Peninsula, we opted to regress M. leprosa against E. orbicularis, although the strength of the statistical relationship between species is the same in both directions. The species-environmental association was assessed using the correlation between species on their response to each environmental variable. Regression analyses were performed separately for each environmental variable and the resulting *t*-values of the coefficients were then compared between species. Relationships between the two species and between each of the species and individual environmental variables were examined using Linear Regression (LinR) for the species abundance data and Logistic Regression (LogR) for the presence-absence data. The nine terms of a third-degree polynomial of latitude and longitude of the cell centroids (trend surface analysis; Mönkkönen et al. 2004; Pereira & Itami 1991) were also included as explanatory variables in the final equation in order to control for the effect of geographical gradients at large scales (Legendre & Legendre 1998). Except for the analysis performed across the whole of the Iberian Peninsula, at 50 km resolution, finer scale spatial patterns were also controlled using a contagion-term based on a two-order neighbourhood (see Segurado, Araújo, & Kunin 2006 for further details). Regressions were adjusted both excluding and including these spatial terms to assess the uncertainty induced by spatial effects on the magnitude and sign of species and environmental associations. A variable selection procedure based on the Akaike's Information Criterion (AIC) was used to ensure some parsimony in the final variable set.

Fable 1. The five datasets used for the analysis and the correspondent available information.

When possible, we also inferred for association between species in geographical space using null models. Two approaches were implemented. First, we used a randomization approach implemented in ECOSIM (Gotelli 2000; Gotelli & Entsminger 2006), based on the C-score of species occurrence matrix. We performed 5000 randomisations maintaining a fixed number of occurrences of each species and assuming the sites as equiprobable (see Gotelli 2000, for further details). The C-score statistic is based on the proportion of sites for which species A is present and species B is absent and vice versa. Increasing C-score values indicate an increasing degree of mutual exclusion of species. This method was not applicable for the stream reach dataset because one of the species (M. leprosa) occurred in all sampling sites. Inflation of type I errors is expected to occur with this method, since it does not account for the spatial autocorrelation of data (Roxburgh & Matsuki 1999). Therefore, we also ran second null models based on toroidal shifts, which consisted of data permutations that maintained the global spatial structure of the original data (Palmer & Van der Maarel 1995; Segurado et al. 2006). This analysis was only run for the Iberian Peninsula (10 km resolution) and for the stream reach datasets, since the method requires data recorded in regular grid systems without missing data. In order to run toroidal shifts at the scale of the Iberian Peninsula, a rectangular area – as required by the algorithm – with 44 by 60 cells was selected (see Segurado et al. 2006 for further details on the method). One thousand null spatial patterns were obtained for one species and each one was regressed against the spatial pattern of the other species using a linear regression approach. The observed *t*-value of the regression coefficient was then located in the expected distribution of t-values obtained under the null hypothesis in order to obtain the non-randomness probability of the relationship.

Except for the randomisation approach implemented in ECOSIM, all analyses were performed using S-Plus 2000 (Statistical Sciences 1999).

Results

A shift was found from an overall positive association at broader spatial scales to a non-significant or negative association between the species at finer scales (Table 2, Fig. 2). The overall sign and magnitude of the spatial association was generally consistent between the different alternative methods (ECOSIM, toroidal shifts and regression-based approaches; Table 2).

The spatial association between the two species varied among spatial scales. For the Iberian dataset, compiled at a 50 km resolution, a significant albeit non-linear relationship between the species was found; estimated relationships were independent of whether spatial patterns were controlled for or not (Fig. 2A and B). By either method, a positive relationship was the general trend, as shown by the positive sign of the linear term of species occupancy. Both for the Iberian Peninsula with 10-km resolution and for the territory of Portugal at finer resolution (habitat), we found a positive association between the two species that was maintained even after controlling for the spatial pattern and contagion (Fig. 2A and B). For the Southwestern coast dataset, there was a negative association when no spatial covariate term was included, which was cancelled after controlling for the spatial pattern and contagion (Fig. 2A and B). For the stream reach dataset, no significant relationship was found (Table 2), either controlling or not controlling for spatial pattern and contagion (Fig. 2A and B).

The shift from positive to negative association between species with decreasing spatial extents and finer resolutions was more evident when it was based on the comparison of species response to environmental association (Fig. 3). For the three broader spatial extents and coarse resolutions there were significant (p < 0.001) positive relationships found between species in their response to the environment given by the absolute value and sign of the univariate relationship (t-value) between species occurrence and each environmental variable. This positive association was maintained even after controlling for spatial pattern and contagion (Fig. 3A and B). For the Southwestern coast dataset there was a negative association that became non-significant after controlling for the spatial pattern and contagion (Fig. 3A and B). For the stream reach dataset, a consistently significant (p < 0.001)negative association between the occurrence patterns of the two species was found.

Discussion

Our results demonstrate that when patterns of coexistence are examined at different spatial scales, different inferences about the sign of the interactions between species can arise. Assuming that mechanisms of coexistence do not change throughout the considered geographical extent (Iberian Peninsula), the observed variations of patterns of coexistence across scales can be largely attributed to variation in spatial resolution alone. In our study, *E. orbicularis* and *M. leprosa* broadly coexist at coarse resolutions in the Iberian Peninsula. However, the two species segregate when their occurrences are examined at fine resolutions. This result contrasts with a recent study that reports a significant role of biotic interactions at the community level (Danish bird community assembly) across different grain sizes, up to 10-km (Gotelli et al. 2010).

Although generalizations about the importance of biotic interactions in structuring communities across scales are difficult, some trends can be identified from studies focused on the coexistence of pairs of species. For example, pairs of species that show a consistent negative association across spatial scales are typically congeneric and are parapatric, i.e., with geographical ranges that hardly overlap (Anderson et al. 2002; Bullock et al. 2000). Conversely, reported positive species associations at broader spatial scales and segregation at finer scales were often found for sympatric species that

Table 2. *P*-Values for the alternative association tests: $LogR/LinR^* - Logistic Regression/Linear Regression ($ *t* $-test significances of the regression coefficients); <math>LogR/LinR^{**} - controlling$ for the spatial pattern and contagion; ECOSIM (probability of the observed C-score to be equal or higher than the expected under the null pattern); TOROID (probability of the observed *t*-value of the regression coefficient to be equal or higher than the expected under the null spatially structured pattern). (+) and (-) means, respectively, positive and negative coefficient values. Blank cells means that the method was not applicable for the dataset.

Dataset	LogR/LinR*	LogR/LinR**	ECOSIM	TOROID
Iberian Peninsula 50 km	<0.001 (+)/0.010 (-) ^a	0.002 (+)/0.042 (-) ^a	<0.001 (+)	_
Iberian Peninsula 10 km	<0.001 (+)/-	<0.001 (+)/-	<0.001 (+)	< 0.001 (+)
Portugal habitat	0.638/-	0.634/-	< 0.005 (+)	_
South-western coast habitat	0.003 (-)/-	0.052 (+)/-	< 0.001 (-)	_
Stream reach microhabitat	0.783/0.493 ^a	0.387/0.299ª	_	0.764

^a*P*-Value of the quadratic term of species abundance (see text for details).

were phylogenetically dissimilar, while showing overlap of their general ecological requirements (Firth & Crowe 2010; Pita, Mira, & Beja 2011).

At broader spatial scales, it is difficult to infer the sign of the biotic interactions by simply examining patterns of co-occurrence between species, although the mere existence of systematic co-occurrence across species ranges indicates that some type of direct or indirect interaction is possible (Araújo, Rozenfeld, Rahbek, & Marquet 2011). When analyses are undertaken at coarse spatial resolutions, sample units will contain greater environmental heterogeneity and this provides opportunities for sympatry even for competing species (Araújo & Guisan 2006; Connor & Bowers 1987). On the other hand, at larger spatial extents there is a possibility that biotic interactions are masked by the effect of similar physiological responses to broad climatic gradients. This factor explains why, at wide geographical scales, species distributions can be largely explained by abiotic variables alone (Soberón 2010).

Positive associations between species distributions might be expected among pairs of species that were exposed to similar phylogeographic constraints in the past and/or interact through mechanisms of facilitation. Even though the two studied Iberian freshwater turtle species evolved



Fig. 2. Spatial association between *E. orbicularis* and *M. leprosa* for each of five spatial extents and resolutions considered; (A) response curves not controlling for space, (B) partial response curves controlling for spatial pattern and contagion (see "Materials and methods" for further details). All *y*-axes are in the scale of the centred linear predictor. Data points are partial deviance residuals. See Table 2 for the statistical significance of the relationships (NS, non significant).



Fig. 3. Relationship between species' response to environmental variables based on the *t*-values of univariate regressions of species occurrence versus each environmental variable: (A) relationship not controlling for space, (B) relationship controlling for spatial pattern and contagion (see "Materials and methods" for further details). All regression analyses are significant (p < 0.001) except NS.

independently, they show similar physiological, behavioural and dispersal limitations. Therefore, their actual distribution probably reflects similar historical constraints. If facilitation was responsible for the positive association at coarse scale, this trend should hold true for finer spatial scales, which is not the case.

At smaller spatial scales and finer resolutions, differences in the use of space by species seem to depend upon specific local conditions. In our study, the two local scale datasets where a negative association between species was observed correspond to rather distinct landscapes. In the Southwestern Portuguese coastal zone, the species segregate at the habitat level. E. orbicularis is almost entirely restricted to the temporary ponds in a coastal strip, while M. leprosa is restricted to streams and permanent ponds in the inland zone. Since habitat gradients are coincident with a spatial gradient (inland versus coastal zone), a considerable amount of the explained variation in the data is possibly shared by the environmental and the spatial variables. Consequently, a large proportion of variation attributable to the environmental gradient was cancelled when the effect of space was included in the association test, such that it is very difficult to infer whether species have a true negative environmental association. In contrast, the sampled stream lies within a relatively homogeneous landscape

even though spatial heterogeneity exists along the stream at finer resolutions. In this case, species tend to be segregated at the microhabitat level and our results suggest that *E. orbicularis* occurs in temporary and shallow reaches, while *M. leprosa* is less selective regarding microhabitat, although tending to occupy permanent and deeper reaches of the stream segment. The association of *E. orbicularis* with seasonally dry habitats in both regions (and the contrasting preference of *M. leprosa* for permanent water bodies) suggests that the negative environmental association observed in the Southwestern Portuguese coast is not explained solely by spatial segregation.

Whether this segregation is the result of different habitat preferences or shifts induced by biotic interactions between the species remains unanswered. It is also possible that strong interspecific competition occurring in the past has resulted in genetically determined differences in habitat selection in the present. Further studies based on manipulative experimental designs directed specifically to the inference of the role of biotic interactions (e.g. Abramsky & Sellah 1982) are needed to test these alternative hypotheses.

Nevertheless, our results contrast with the few quantitative studies on habitat selection by *E. orbicularis* in Europe, in regions where *M. leprosa* is absent. For example, the preference for large permanent water bodies and lower courses of large permanent rivers is documented, respectively, for the Po River delta of northern Italy (Ficetola et al. 2004) and in the southern region of European Russia (Bozhansky & Orlova 1998). This contrast may be due to different local adaptations of the species or may reflect different biotic constraints (e.g. competitive interactions) in distinct parts of its geographical range.

A possible effect of data uncertainty, namely regarding the absence data, cannot be ruled out (Dormann, Purschke, Márquez, Lautenbach, & Schröder 2008). A main source of bias could be due to the secretive character of *E. orbicularis* in comparison to *M. leprosa*. This problem would be more pronounced at geographical scales, since data were mainly compiled from distribution atlas that were essentially based on generalist sampling schemes not specifically directed to these species. At finer spatial scales, since species-specific sampling effort was used, this source of bias can be neglected. The main bias introduced by this problem would be that false absences might arise in the data, i.e., species would coexist more frequently than suggested by the available data. As a result, the positive association found at the geographical scale would even be more pronounced.

This study suggests that potential biotic interactions may not be properly inferred at broad spatial scales and that multiscale approaches are crucial to fully explore patterns of co-occurrence and to construct accurate hypotheses about the relative importance of biotic interactions. Therefore, proposed frameworks to infer mechanisms underlying spatial patterns (e.g. Anderson et al. 2002; Araújo et al. 2011; Gotelli et al. 2010; Sfenthourakis et al. 2005) should take into account the possibility that the relative importance of mechanisms of co-occurrence might change at different spatial extents and resolutions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2012.03.008.

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