Web Ecology 4: 14–21.

Trends in the evolution of ecology: "Spain is different"

Adolfo Cordero Rivera

Cordero Rivera, A. 2003. Trends in the evolution of ecology: "Spain is different". – Web Ecol. 4: 14–21.

During the last fifty years ecology has matured as a scientific discipline. In this paper I analyse the temporal development of the paradigm based on physical systems (the ecosystem paradigm), and the evolutionary ecology paradigm. I first analyse the contents of 61 textbooks to calculate the relative importance of ecosystem and evolutionary ecology in the training of new generations of ecologists. Results indicate that the evolutionary approach is becoming more important since 1980, and now most textbooks dedicate 10–20% of their pages to evolutionary concepts. In a second analysis I searched the names of ecology departments in universities around the world, and found out conspicuous differences between USA, where 43% of addresses associate ecology and evolution or behaviour on the same department, and Europe, where only 10% of ecology departments also include a reference to evolution or behaviour in their name. In both analyses Spain seems to follow only the ecosystem paradigm, because Spanish textbooks dedicate almost no pages to evolutionary concepts, and there is not a single university department that includes ecology and evolution. A further bibliometric study confirmed that Spanish ecologists prefer to publish their research in general ecology journals, and are under-represented in evolutionary ecology journals. I discuss the importance of historical factors on the development of paradigms of ecology, and the special case of Spain, likely due to the influence of pioneers working in oceanography, limnology and geography.

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Ecology has been defined in multiple, contrasting ways. Some stress the biotic component, i.e. "Scientific Natural History" (Elton 1927), while others are more attracted to the "system" concept and therefore to abiotic analogies (Odum 1992). Ecology has been also defined as the least biological of all biological sciences (Barbault 2000). This division is probably at the heart of ecology and explains its polyphyletic origin (Weiner 1995). Cherret (1989) showed that ecologists are either reductionists or holists, and the debate between the two schools has been highly productive (McIntosh 1985, Peters 1991, Real and Brown 1991, Aarssen 1997, Lawton 1999, Keller and Golley 2000). Nevertheless, there is a clear tendency to a synthesis of both approaches in recent years. As an example, the journal Ecology now accepts papers on "physiological responses of individual organisms to their biotic and abiotic environments, ecological genetics and evolution, the structure and dynamics of populations, interactions among individuals of the same or different species, the behavior of individuals and groups of organisms, the organization of biological communities, landscape ecology, and ecosystems processes" (the emphasis is mine).

Accepted 22 October 2003

ISSN 1399-1183

The ecosystem concept (or even the thecno-ecosystem; Odum 2001), and especially its emergent properties are at the centre of this polemic. Some ecologists defend that ecology should move toward physics, and use machine analogies when study ecosystems (e.g. Margalef 1980, 1995,Odum 1980). This approximation to ecology was very characteristic in the first steps of the ecosystem research agenda (Golley 1993). Nevertheless, "Ecosystem ecology" is controversial because "research has failed to develop a theory associated with whole systems rather than their component parts" (Goulden 1994, but see Ulanowicz 1997).

"Evolutionary ecology" (Pianka 2000, Fox et al. 2001) is the new paradigm that has attracted the attention of many ecologists, especially those studying populations and behaviour. Evolutionary biology plays a central role in the complexity of biological systems because evolution is the source of biocomplexity, and therefore it has been claimed that research on evolution is crucial to solve ecological problems (Meagher and Futuyama 2001). Furthermore, evolution and adaptation are special characteristics of biological systems that are not found in physical systems, and failing to recognize this fact led to many negative effects on the history of Biology (Mayr 1998).

An ecosystem concept void of evolutionary content has been clearly dominant in the history of ecology, but there seems to be a trend toward more evolutionary approaches in recent years (Golley 1993)."Scientific ecology is grounded in several fundamental principles, including the principles of system and evolution. System is concerned with the question: How does it work? Evolution is concerned with the question: How did this system come to be this way?" (Keller and Golley 2000). Unfortunately, the relationship between ecology and evolution has been highly conflictive, particularly under the ecosystem approach (Loehle and Pechmann 1988, Golley 1993).

In this paper my aim is to identify paradigm shift in ecology (Kuhn 1971). Specifically I am interested in studying whether the evolutionary ecology paradigm has attracted the attention of the new generations of ecologists. Thus, this paper aims to answer the following questions: Is there any temporal trend in the relationship between ecology and evolution? If so, is this trend universal? My results suggested that Spanish universities are a conspicuous outlier in ecological research. For this reason I made a further bibliometrical analysis of research published by Spanish ecologists, but I think that a similar situation is likely to be true of other countries. This analysis illustrates the effect of social and historical factors on the development of ecological science.

Methods

An analysis of ecology textbooks

One way to study paradigm shifts in science is to analyse textbooks (e.g. Alcock 2003). Textbooks are used to educate future researchers, and therefore are clear examples of the personal interpretation of the "essence" of ecology of each author. This is especially important when textbooks are scarce, like in the beginning of a science. For instance Fundamentals of ecology of E. P. Odum had a tremendous didactic impact until competitive textbooks appeared (Golley 1993).

For this analysis I examined the table of contents of 61 textbooks published between 1953 and 2002 (the only exception was Elton's book published in 1927 and listed in the Appendix). I included in the analysis all the books I could find, but I excluded all books with a clear ecosystem orientation (e.g. forest and marine ecology books), as well as all evolutionary ecology and animal or plant ecology textbooks (with the exception again of: Elton 1927, Dowdeswell 1959, Terradas 2001). These books are listed in the Appendix.

I calculated the percentage of evolutionary ecology in each textbook by page numbers. I used a narrow definition and counted as "evolutionary" all pages dedicated to adaptation, evolution, population genetics, life-history strategies and behavioural ecology. The percentage of "ecosystem" ecology was calculated from the percentage of pages dedicated to biogeochemical cycles, energy, production and biomes. Books were classified as "American", "European" and "Spanish" based on the country of publication of the original edition.

I used a Generalized Linear Model (GLM) with binomial errors in the response variable (number of pages of evolutionary or ecosystem concepts), the total number of pages as binomial denominator and logit link (Crawley 1993), to test for temporal trends and regional effects. Overdispersion in the model was corrected with the extrabinomial procedure in GenStat (Anon. 2000). I entered date of publication and region of publication (i.e., America, Europe, Spain) as independent variables.

Is ecology associated to evolution? An analysis of the names of ecology departments

To test whether ecology and evolution are considered related disciplines in different countries, I searched the names of ecology departments using Biological Abstracts for 1999–2000. I was looking for the names of university departments only, and therefore other institutions were not included. The reason was to restrict the analysis to educational institutions. The selection criterion was: DEPART* AND ECOL* AND UNIV* IN AD (the asterisk searches for any letter, and AD is the tag for the address field). This search provided a total of 3181 records. I realised that the results did not include many Italian and French-speaking addresses, due to the spelling of "Département" and "Dipartimento" that did not match the search criterion. Therefore, I completed the search by looking for these addresses with additional searches (this correction was not needed for other countries because addresses were usually written in English). I found a total of

3463 records (i.e. papers) by 433 addresses, but restricted the analysis to countries that had at least five addresses (371 addresses of 22 countries).

Publication preferences by Spanish ecologists

Given the differences between ecology textbooks written by Spanish authors and the rest of nationalities (see Results), it is important to find out a plausible cause, and likely consequences. If textbooks reflect the training of new generations of ecologists, I expect Spanish ecologists (defined here as researchers working in an ecology area of a Spanish university) to have different research interests than other ecologists. This is clearly difficult to measure. One way to approach this problem is to check the journals in which Spanish ecologists publish their research.

I searched again Biological Abstracts (from the second half of 1995 to the first trimester of 2002) for papers published by Spanish researchers (given that only the address of the first author is found in the database, this search does not include papers published by Spanish authors in post-doctoral stays or when the Spanish author is not the first author) in 14 ecology journals. Nine journals were classified a priori as "evolutionary or behavioural" (Trends in Ecology and Evolution, American Naturalist, Evolution, Evolutionary Ecology, Journal of Evolutionary Biology, Biological Journal of the Linnean Society, Animal Behaviour, Behavioral Ecology and Sociobiology, Behavioral Ecology) and five as general journals (Oikos, Ecology, Journal of Animal Ecology, Journal of Ecology, Oecologia). If Spanish scientists select their journals "at random" I expect them to publish the same proportion of their work in both types of journals. I analysed the number of papers published by Spanish researchers in both types of journals using a GLM with binomial errors and logit link with the number of papers by Spanish authors as the dependent variable, the total number of papers as binomial denominator and the type of journal (evolutionary/general) as a factor.

To test for publication bias in Spanish ecologists from educational institutions, I repeated the above analysis including papers authored by scientists whose address was in the ecology area of a university.

Results and discussion

Temporal trends in ecology textbooks

The proportion of evolutionary ecology in text books was related to time and country of publication (Fig. 1A, B; deviance ratio = 5.69, $p = 0.002$). There was a clear increase in evolutionary content with time (year effect; $t = 2.42$, $p = 0.016$). Using American textbooks as the reference group, there were no differences between American and European books ($t = 0.22$, $p = 0.826$), as opposed to Spanish books, which followed the opposite tendency ($t = –2.34$, $p = 0.019$; Fig. 1B). This analysis is not fully correct because some books were written by the same authors, and therefore their contents are unlikely to be independent. Nevertheless two tendencies are clear from Fig. 1 when different books written by the same author are compared: authors that started with a very low coverage of evolutionary ecology increased it over the years (Odum and Molles are the best examples), whereas those that started with a very high coverage diminished it (e.g. Ricklefs and Stiling). Both schools converged to a content of evolutionary ecology around 10–20% (Fig. 1A).

There were no clear temporal tendencies in the ecosystem ecology contents (Fig. 1 C, D). The model was not significant (deviance ratio = 1.92, $p = 0.137$), nor was the effect of date of publication ($t = –1.41$, $p = 0.159$), or the difference between America and Europe ($t = 0.10$, $p = 0.920$), but Spanish textbooks were again significantly different from American books, in this case due to an increase in ecosystem content ($t = 2.09$, $p = 0.037$).

An analysis of the names of ecology departments

Figure 2 shows the percentage of ecology departments whose name also includes "evolution" or "behaviour". There are conspicuous differences between countries (Fig. 2): 43% of USA addresses (34/79) associated ecology and evolution, but not a single address did the same in six countries. In European countries ecology is associated with evolution in 10% of addresses (20/172, Spain excluded). This value is significantly lower than in the USA ($\chi^2 = 35.3$, DF 1, $p < 0.001$), but not significantly different from Spain (0/26; ($\chi^2 = 1.86$, DF 1, $p = 0.172$). The case of Spain is striking because it is based on 26 addresses (i.e. included almost all ecology departments in Spanish universities). For this reason I searched the web pages of all 33 Spanish universities that have ecology areas (in Spanish universities the basic unit is the "area" of knowledge. "ecology" and "genetics" are considered areas, but neither "evolution" nor "ethology" are included in this classification. Nevertheless the name of a department is not restricted to the name of the areas it includes. Departments are responsible for teaching in one or several faculties) and found out that ecology is usually associated to zoology or botany, but only in five cases is in the same department as genetics, and in one case ecology is in the department of physics (surprisingly together with "Theoretical physics" and "Astronomy and astrophysics" among other areas of physics).

"Spain is different"

The analysis of publication preferences by Spanish scientists suggests that they are working in both paradigms: sys-

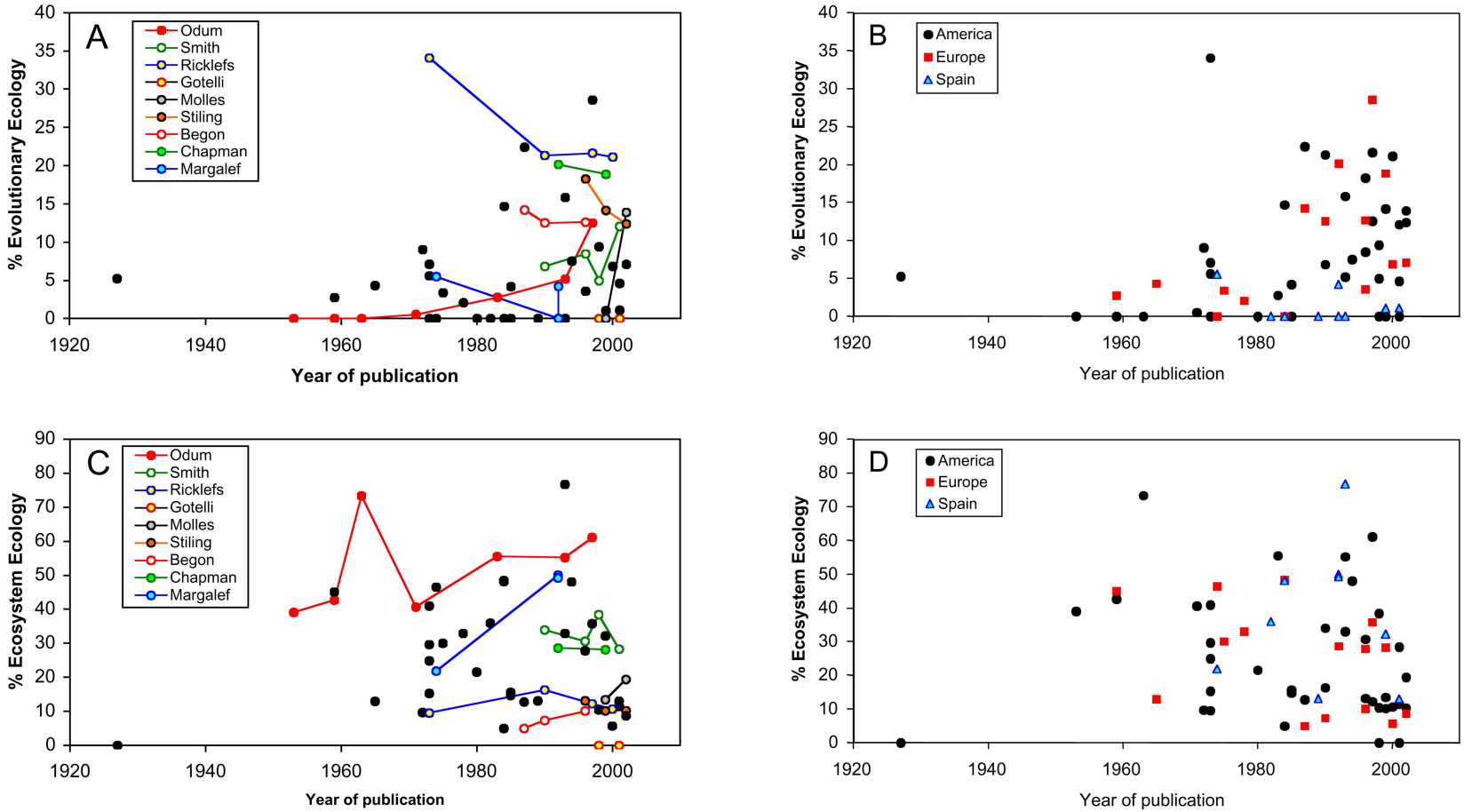

Fig. 1. The relative importance of (A, B) evolutionary ecology (adaptation, evolution, population genetics, life-history strategies and behavioural ecology) and (C, D) ecosystem ecology (biogeochemical cycles, production and biomes) in textbooks of ecology. In panels A and C books writen by the same authors are conected by lines. In panels B and D the same data are categorized by region of publication (America, Europe excluding Spain, Spain). There is a significant increase in evolutionary ecology contents with date of publication in American and European books, but no temporal effect on ecosystem ecology contents. Spanish textbooks follow a negative tendency in evolutionary ecology and a positive tendency in ecosystem ecology.

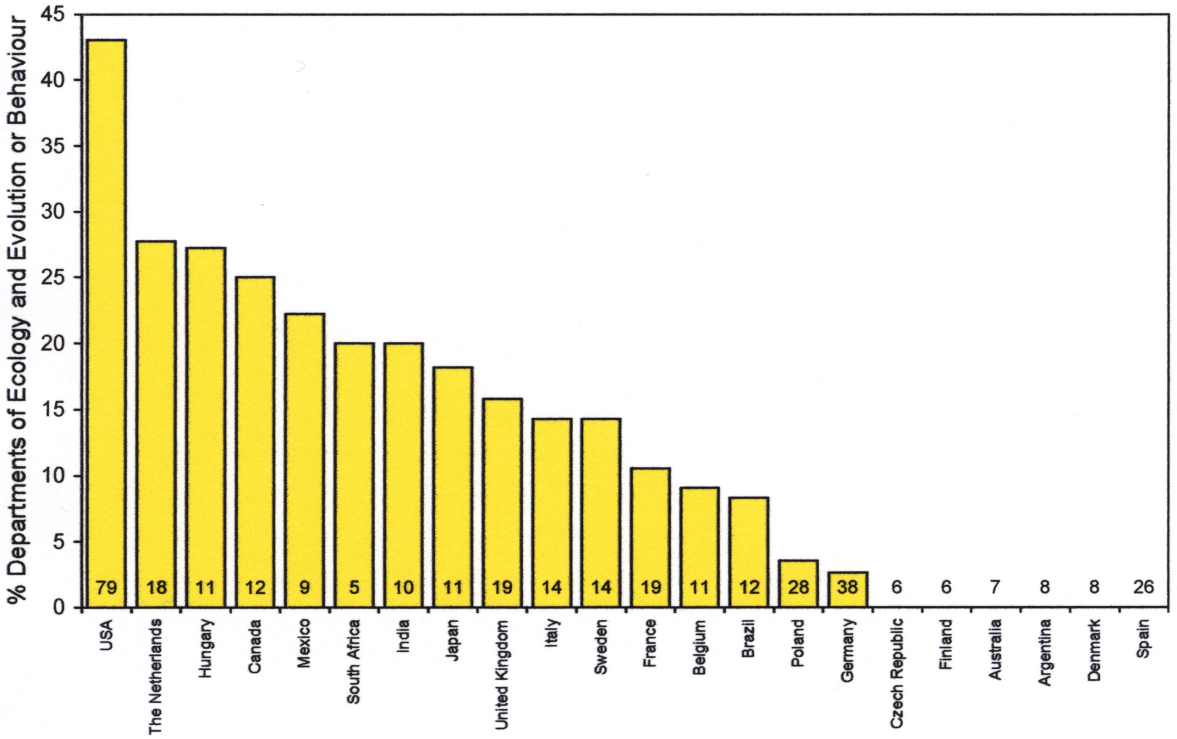

Fig. 2. The proportion of university departments whose name includes ecology and evolution or behaviour in different countries. This figure is based on 3463 papers published by 433 addresses. Numbers inside bars indicate the number of departments examined in each country.

tems and evolutionary ecology (Fig. 3). In fact, 2.7% and 2.2% of papers published by evolutionary and general ecology journals in that period were authored by Spanish scientists, suggesting that there is no publication bias. A GLM indicated that the type of journal did not have any effect on the proportion of papers published by Spanish scientists (deviance ratio = 0.63, p = 0.443; overdispersion was corrected with the Extrabinomial procedure in GenStat).

Nevertheless only a fraction of the papers published by Spanish authors in these journals came from ecology areas in the universities, the others being authored by scientists from other areas in universities or research institutions. In this case there was a clear preference: Spanish ecologists authored 41.3 ± 2.9% of Spanish papers in general ecology journals, while only 9.4 ± 4.0% in evolutionary ecology journals. The GLM was in this case is highly significant (Fig. 3; deviance ratio = 15.20, p = 0.002).

This difference can be even found between two very similar journals. For instance *Ecology* and *Evolution* had an ISI impact factor almost identical in 2000 (3.650 and 3.632 respectively), published almost the same number of papers (1699 and 1443 in the period analysed) and are published in the same country (USA). Spanish scientists contributed to both the same proportion (27 and 30 papers; $\chi^2 = 0.76$, p = 0.383), but Spanish ecologists did not publish any paper in *Evolution* whereas they published 13 papers in *Ecology* ($\chi^2 = 9.92$, p = 0.002). The only reason that I can imagine for such a difference is that Spanish ecologists do not consider *Evolution* as an ecological journal.

Conclusions

The above analyses can be summarised as follows: 1) Ecology is "evolving" to incorporate evolutionary contents in textbooks, a clear example of paradigm shift. 2) This trend is similar for American and European books, but not for Spain. 3) Spanish universities do not associate ecology and evolution, and Spanish ecologists typically do not publish in evolutionary ecology journals.

Historical and social factors can deeply influence the development of scientific paradigms (Deléage 1993). The above analyses suggest that the general pattern in the rise of evolutionary ecology is not universal: Spain seems to be an exception, but further analyses would reveal if the situation is also exceptional in countries with very few "ecology and evolution" departments (Fig. 2). In the 1970s the slogan "Spain is different" was used by the Spanish government to

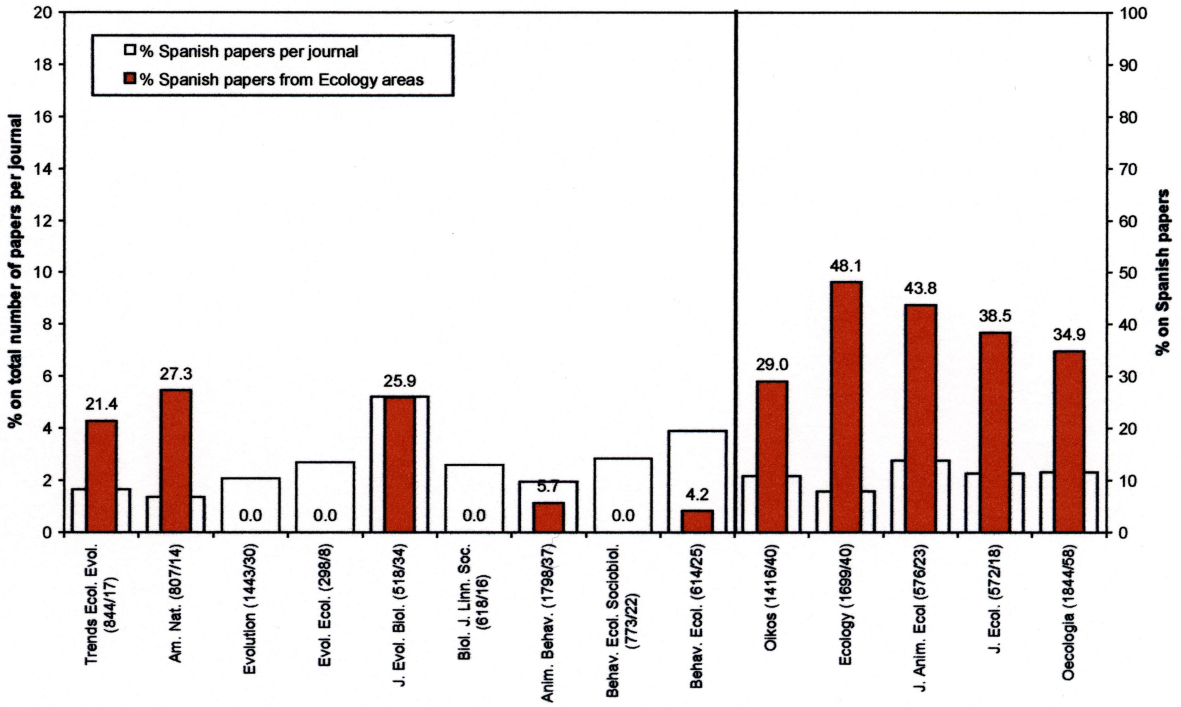

Fig. 3. An analysis of publication bias by Spanish scientists and ecologists. Journals to the left of vertical line were defined as "evolutionary or behavioural", and those to the right as "general". Spanish scientists contribute to both types of journals in the same proportion (left axis, open bars; the number of papers analysed and the number authored by Spanish scientists is indicated in parenthesis after the name of the journal), but Spanish ecologists clearly avoid evolutionary journals (right axis, closed bars; proportion of papers authored by scientists from ecology areas on total of papers published by Spanish authors).

attract tourism. Several authors have suggested that Spain is also different in research organisation, especially because of the high inbreeding rate: most positions in universities are obtained by people trained in the same university (Camacho 2001, Soler 2001, Navaro and Rivero 2001).

It is tempting to speculate for a reason explaining these differences. The first steps of ecology in Spain were clearly influenced by the evolutionary thinking of some pioneers, but this fact rapidly changed and already in the second decade of the 20th century evolution did not play any significant role on Spanish ecology (Casado de Otaola 1997). The first Spanish Ecologists were clear examples of ecosystem research scientists with very few evolutionary interests, perhaps because all of them were limnologists, oceanographers or geographers. The tremendous influence of R. Margalef's textbook "Ecología", first published in 1974 (Margalef 1982), is perhaps one of the causes of the above mentioned absence of evolutionary thinking among Spanish ecologists. Yet, this textbook dedicated 5.5% of 908 pages to evolutionary concepts, which is the maximum in Spanish textbooks until now. Another possible cause of the lack of evolutionary thinking in Spanish ecologists is the high rate of inbreeding in Spanish universities (Soler 2001, Navaro and Rivero 2001). Given that most of the pioneers in ecology were ecosystem ecologists, and most of the positions were won by their students, evolutionary thinking is almost absent from ecology areas in Spanish universities. This occurs not only in ecology but is a general trend in Biology in Spain: there are very few courses on evolution in Spanish universities (Soler 2002), and therefore biologists are poorly trained in evolutionary theory. Most (2/3) of students of biological sciences in Spain still use Lamarckian thinking in their second year of university (Jiménez Aleixandre 1991).

This analysis of paradigms in ecology suggests the influence of social and historical factors in the development of a science, and parallels the evolution of animal behaviour as a discipline (Alcock 2003). Only one department of evolutionary ecology is found in the Spanish system of research (not included in any university, but in the National Museum of Natural History at Madrid), and in agreement with the above analyses the name of this department was due to a Spanish scientist educated in USA.

Modern ecology is now evolutionary, even for topics traditionally treated as free of Darwinian influence, like ecosystem functioning (Tilman 2001) or plant defence chemicals (Hamilton et al. 2001). New textbooks emphasise evolution as a basic component of Ecological concepts, even for a general course of ecology. Some complain by the scarcity of evolutionary ecology textbooks (Siepielski et al.

2002). Nevertheless my analysis suggested that we might no longer need evolutionary ecology textbooks, because most authors have changed their approach to teaching ecology from an evolutionary point of view. I only hope that this change will also take place in Spain. As a consequence of the analyses hitherto presented, my address now includes "Evolutionary Ecology Research Group", given that I cannot change the name of my department.

Acknowledgements – I thank Manuel Soler, Juan José Soler, Montserrat Gomendio and Frank Johansson for constructive criticism on previous versions of this paper.

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Appendix. Ecology books used. List in chronological order.

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