HIGHLY ADAPTABLE BUT NOT INVULNERABLE: NECESSARY AND FACILITATING CONDITIONS FOR RESEARCH IN EVOLUTIONARY DEVELOPMENTAL BIOLOGY

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ABSTRACT

Evolutionary developmental biology is a highly variable scientific innovation because researchers can adapt their involvement in the innovation to the opportunities provided by their environment. On the basis of comparative case studies in four countries, we link epistemic properties of research tasks to three types of necessary protected space, and identify the necessary and facilitating conditions for building them. We found that the variability of research tasks made contributing to evolutionary developmental biology possible under most sets of authority relations. However, even the least demanding research depends on its acceptance as legitimate innovation by the scientific community and of purely basic

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research by state policy and research organisations. The latter condition is shown to become precarious.

Keywords: Scientific innovation; emergence of fields; authority relations; life sciences; evolutionary developmental biology

INTRODUCTION

In this article we look at the development of a scientific innovation that in many respects epitomises the varied nature of scientific change. Different from innovations that emerged from specific experiments or methodological developments (see e.g. Laudel et al. in this volume on Bose-Einstein condensation), evolutionary developmental biology (evo-devo) has a much longer trajectory with more diffuse roots. It can be traced back to the end of the 1970s, when it became more and more obvious that neo-Darwinian theory was unable to account for all empirical findings of evolutionary biology (Müller, 2007), particularly the rapid changes in the forms of organisms evident from the fossil record and the origins of traits that did not constitute an adaptation to the environment.

> It became increasingly obvious that these explanatory deficits of neo-Darwinism were due to its treatment of development as a 'black box' and the consequent absence of the generative rules that relate between genotype and phenotype. (Müller, 2007, pp. 500–501)

The discovery of genes regulating embryonic development in the 1980s (HOX genes) and advances in molecular and genomic techniques made it possible to address specific questions by comparing the development of different organisms, which led to increased understanding of developmental mechanisms on the molecular level (Gerson, 2007; Raff, 2000; Müller, 2008). This research recently received a further impulse by a breakthrough in the development of sequencing technologies, which made the sequencing of whole genomes affordable for single research groups.

These conceptual and methodological developments affect a variety of fields. Responses to the new ideas range from purely conceptual developments to complicated experiments. Research in evo-devo can be conducted in many ways, and thus can adapt to specific organisational conditions and authority relations. However, some features of different approaches to evo-devo make them sensitive to organisational conditions, which is why they do not thrive in all organisations and countries.

Evo-devo research can be taken up by researchers from either developmental or evolutionary biology fields by integrating the complementary perspective and can be either theoretical or experimental. Experimental evo-devo research is always comparative but varies in the types of organisms that are used and in the ways in which the empirical evidence about the organisms to be compared is acquired. Most of the research compares two or more species but some scientists compare transgenic organisms belonging to the same species. The organisms studied can be classical model organisms (such as mouse, Drosophila, or Arabidopsis), or they can be selected because they are best suited to answer specific evo-devo questions (e.g. hedgehogs or snakes). The comparisons required by evo-devo research can also take a variety of forms. Many researchers experiment with organisms from one species and acquire information about the organism(s) they use for comparisons either from the literature or by collaborating with colleagues who investigate the other organisms. Others experiment with more than one organism. Most of these possibilities occur in three major fields in which evo-devo perspectives have taken hold, namely zoology, plant biology and palaeobiology.

The resulting combinatorial complexity of intellectual transition paths to evo-devo and their varied intellectual and resource costs for researchers make evo-devo both a very interesting and a very challenging case for sociologists for studying the impact of authority relations on the development of innovations. Evo-devo is a very interesting object of study because researchers can adapt their involvement in the innovation to the opportunities provided by their environment. They can temporarily or permanently choose degrees of involvement whose costs match the niches provided for them by the various interacting organisations. At the same time, this flexibility makes it much more difficult to attribute variations in the development of evo-devo research to specific authority relations: it is not only that they enable or prevent evo-devo research, but they also enable or prevent certain kinds of evo-devo research.

In this article, we take up this challenge by identifying the conditions under which specific research problems of evo-devo biology can be formulated and solved. This amounts to formulating a 'population ecology of research tasks' that in many ways resembles the population ecology approach in organisational sociology (Hannan & Freeman, 1977, 1989). At the same time, we follow Hodgson (2013) who resolved the argument about selection versus strategic adaptation that has arisen in the context of population ecology in exactly the same way as it is done by our empirical object, i.e. by applying an evolutionary developmental perspective. We combine an evolutionary approach that asks which niches enable, support or prevent specific kinds of research tasks with a developmental approach that asks how researchers together with other authoritative agencies co-created these very niches and adapted their research tasks to them.

Analysing the ecology of evo-devo research tasks involves a causal argument consisting of three steps, which we present after introducing the theoretical background and the methodological approach of our research. First, we analyse the epistemic characteristics of different kinds of evo-devo research and identify the kinds of protected space that scientists need for engaging in the various lines of this research. Second, we identify the necessary and facilitating conditions for building these kinds of protected space and the authoritative agencies controlling them. This analysis enables a third step, in which we ascertain how researchers could build protected space in different countries.

THEORETICAL BACKGROUND

The emergence of fields (or scientific specialties, as they were called at that time) enjoyed much attention in the sociology of science during the late 1960s and 1970s.[1] Inspired by Kuhn, analysts attempted to identify relationships between cognitive dynamics and social patterns in the early stages of development. Focusing on the link between the dynamics of ideas and patterns of interaction, the studies of emerging scientific specialties did not pay much attention to the conditions under which the research was conducted and the opportunities for changing research practices provided by these conditions. In 1976, Edge and Mulkay produced a synopsis of studies of emerging specialties that identified three common features of specialty emergence: the growth of the specialties from innovations at the margins of established disciplines, the mobility of researchers, and ready access of the proponents of the new specialties to graduate students (Edge & Mulkay, 1976).

Evo-devo does not, though, fit these patterns because research in this area grows on top of, rather than beside, existing fields. The differentiation pattern observed in the cases studied in the 1960s and 1970s was one of 'branching' according to which new research areas emerged around new sets of problems, research technologies, or empirical objects (Mulkay, 1975). By contrast, evo-devo adds a new layer of empirical research and a new frame of reference in which experiments can be designed and data compared. This means that moves of researchers from old to emergent fields can be partial and may be reversed.

The early studies of emerging fields also had a rather narrow focus in that they did not link the observed social conditions for emergence to organisational or policy decisions. This might have been due to the different situations of scientists at the time the fields emerged, particularly regarding access to research funds and tenured posts. Most of the researchers in these studies were already on permanent contracts, had relatively easy access to resources, and were able to move between universities as opportunities arose. Once established in tenured posts, they were much less dependent on authorities (organisational managers, disciplinary elites and external agencies) than are their colleagues today.

More recent science policy studies that look at the shaping of emergent fields (such as nanotechnology) by governance structures typically take the reverse perspective. They look almost exclusively at policy measures channelling resources to emerging fields and trying to influence the directions of their development (see Gläser et al., 2014 for a critique). Scientific innovations that do not attract political attention, e.g. due to lack of potential for applications, and the processes through which governance structures and processes affect the development of fields do not tend to be the focus of these analyses.

Investigating the evolution of evo-devo research links the problem choices of researchers to the niches created by contrasting governance structures in different countries. We consider evo-devo as a scientific innovation, which we define as a research finding that affects research practices (choices of problems, methods or empirical objects) of a large number of researchers in one or more fields.[2] Changing research practices incurs costs and maybe risky, e.g. by devaluing knowledge, equipment and reputation accumulated with previous research. Our comparative framework focuses on differences in authority relations (Whitley, 2010) as the key mediating factor connecting governance structures to changes of research practices, and uses the concept of protected space (Gläser et al., 2014; Whitley, this volume) to compare the opportunities for researchers to change their practices under the specific conditions created by different sets of authority relations.

The state, research organisations, external funding agencies and scientific elites exercise authority over research choices through three main channels: control of resources, the allocation of reputation and the provision of career opportunities. For these channels the relative authority of each set of actors can be assessed, and a framework for the comparative analysis of everyday governance of research activities formed accordingly. This framework can be linked to the micro-level of changing research practices by identifying the authority relations that conditioned how researchers attempted to move to evo-devo research.

The impact of particular sets of authority relations on the opportunities for changing research practices towards evo-devo can be ascertained by comparing the level of protected space that is required for different kinds of changes with the level that can be built by researchers in different sets of authority relations. We define protected space as the *autonomous planning horizon for which a researcher can apply his or her capabilities to a self-assigned task*. The two critical dimensions of this variable are the *time horizon* for which the capabilities are at the sole discretion of the researcher, and the *resources* (including personnel over which the researcher has authority and the actual time available for research). Researchers create and extend protected space mainly by career decisions (the search for positions that provide protected space), negotiations with managers of their research organisation, and the acquisition of funding. Important dimensions of this last variable are the likelihood of success in receiving funding and the speed with which such funding can be obtained.

METHODS AND DATA

We use data from the larger comparative project that studied the impact of changing authority relations in four countries on conditions for intellectual innovations that is summarised in the editorial introduction. Through searches in publication databases (Web of Science, Google Scholar) and Internet webpages we detected research groups who had included evo-devo into their research portfolio. We also asked our interviewees which other evo-devo researchers in their national community they were aware of. In Sweden, Switzerland and the Netherlands most evo-devo researchers could be interviewed. In Germany with its large evo-devo community, only selected cases could be investigated. Researchers who presented evo-devo as a research focus on their websites were selected, taking into account the variation of disciplines (zoology and plant biology) and of types of research organisations (university and public research institute). Additional information was obtained by interviewing experts in the field, and heads of faculties and institutes. The distribution of our interviewees is summarised in Table 1. The table also lists the situations we investigated as cases, namely situations in which researchers successfully or unsuccessfully attempted to build protected space. Not all of our interviewees undertook

Table 1. Overview of Interviews and Cases.

	Germany	Netherlands	Sweden	Switzerland
Researchers	7 group leaders	11 group leaders	3 group leaders	7 group leaders
	1 PhD student	2 PhD students	2 postdocs	5 postdocs
Other informants	–	3[a]	–	4[b]
Total number of interviews	8	16	5	16
Number of transition situations	12	13	7	9

[a]One researcher who gave background information on the evo-devo field, one director of an institute, one officer of a funding agency.
[b]One evo-devo background, three heads of institutes or deans of faculties.

these attempts; some of them were postdocs whose research was determined by the decisions of their group leaders. Furthermore we consulted self-descriptions of the evo-devo community on the development of the field (e.g. Carroll, 2006; Hall, 2012; Laubichler & Maienschein, 2007; Minelli, 2008; and the authors quoted above).

The interviews with researchers consisted of two main parts. In the first part, the interviewee's research that contained the innovation was discussed in the context of the interviewee's research projects, exploring the continuity and all thematic changes and reasons for them. Parallel developments in the interviewee's national and international communities were also discussed. The discussion of the content of scientists' research required the development of the interviewers' knowledge to an 'advanced layperson's' level and the negotiation of a level of communication at the beginning of the interview (Laudel & Gläser, 2007; see also Collins & Evans, 2002 on the level of expertise necessary for competent interaction). Therefore, it was prepared with Internet searches and publications at various levels of difficulty (from popular science up to an interviewee's publications) were used. Interview preparation also included a bibliometric analysis of the interviewee's publications that enables the identification of thematically linked publications. A visualisation of this publication network (see Fig. 1) was used to 'stimulate the recall' (Dempsey, 2010) and to prompt narratives about the content of research (Gläser & Laudel, 2009).

In a second part of the interview, conditions of research and the factors influencing them were discussed. Topics included the knowledge, personnel

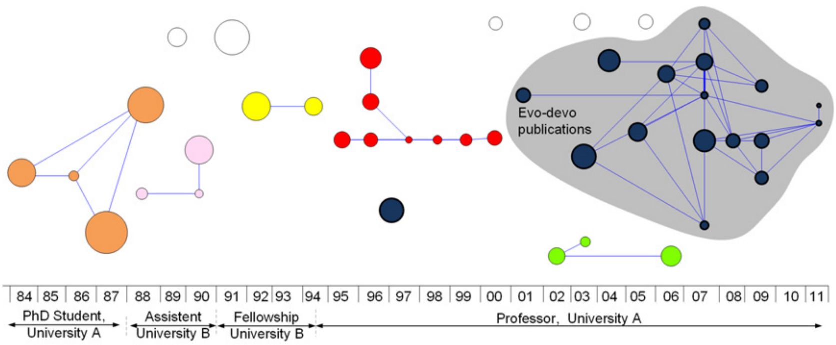

Fig. 1. Example for a Research Trail of an Evo-Devo Researcher (the circles are publications, the size of the circles indicates the number of citations, the lines show thematic connections between publications).

and equipment required to conduct evo-devo research, sources of material support, and opportunities as well as constraints provided by the interviewee's organisational positions. The separation of the discussions of these conditions of research from the content of research is important because it limits the extent to which interviewees present their own subjective theories about how current funding conditions made them conduct their current research. The interviews lasted 60–120 minutes. They were recorded and fully transcribed.

For the comparison we developed typologies for evo-devo practices, transition situations and protected space. In order to deal analytically with the task of identifying influences of authority relations on intellectual transition patterns, we reduced the complexity of these patterns in two subsequent steps. First, we used the combinations of variables with the strongest influence on transition costs to identify ten common transition situations to start evo-devo. In a second step, we allocated these situations to different categories on the basis of the level of protected space they required.

'THE SNAKE TOOK US ABOUT THREE YEARS' – TRANSITIONS TO EVO-DEVO

In order to identify the impact of authority relations on transitions to evo-devo we must first establish what kind of transitions could take place and what protected space these transitions required. The difficulty, cost and risks of a move to evo-devo depended on the epistemic properties of the move, which included properties of the research task chosen by a researcher and the researcher's disciplinary background. We derive the protected spaces necessary for a transition in two steps. First, we identify the properties of transitions to evo-devo that affected the necessary protected space. Second, we distinguish between large, medium and small levels of protected space that the transitions required.

Properties of Transitions

Four properties of transitions to evo-devo research that affected the necessary protected space included (a) the empirical strategy, (b) researchers' original disciplinary background, (c) the types of organisms used for experiments and (d) the approach to comparisons. The combined variation of these properties produces the enormous variance in evo-devo research tasks and associated necessary protected spaces.

Empirical Strategy

One of the most important distinctions for the transition to evo-devo research was that between experimental evo-devo research tasks and other forms of evo-devo research (Table 2). The easiest way to engage in evo-devo research, and one that was the entry ticket to evo-devo for many of our interviewees, can be described as conceptual extension. Conceptual extension occurred when researchers continued their evolutionary biology or developmental biology research line, including the presentation of their

Table 2. Empirical Strategies Affecting the Protected Space Required for Transitions to Evo-Devo.

Empirical Strategies	Impact on Dimensions of Protected Space	
	Resources	Time horizon
Conceptual extension	None	Low
Theoretical research	None	Low
Bioinformatics research	None	Low
Experimental research	Depends on other properties	Depends on other properties

findings to traditional audiences, and used evo-devo as an additional theoretical framework in which they contextualised their findings. This 'dual use' of experimental research for traditional and evo-devo questions did not require any changes in experimental strategies or designs. It only required that the researchers acquire the evo-devo theoretical framework and concepts, and look for possible comparisons of their findings in a more systematic manner.

> A: We just searched the literature and found that there were similar things and we discussed them. We [developmental biologists] never decided to go in the evo direction in fact. But the evo dimension is always involved in what we are doing. So, […] in presentations and seminars it is often discussed, but we are not approaching that directly.
>
> Q: Why didn't you decide to go more into the evo direction?
>
> A: Because we are quite focused, we have all the tools and genetic resources to go on approaching these questions in the mouse, and we have nothing to approach it in another system. We keep contact with these other groups because if they would have tools in the system to test the hypotheses that comes from all that, that would be nice. But I don't think, we will do it ourselves. You cannot become excellent in everything. We are specialized in mouse.[3]

Evo-devo research could also be theoretical in the sense of purely conceptual development, i.e. not linked to experiments at all. A third variant of non-experimental evo-devo is mathematical modelling in bioinformatics, which is conducted either with biological data or by building more abstract models. For a biomathematician, beginning to model evo-devo processes requires the transfer of mathematical skills to new questions.

The empirical strategy chosen affected mostly the resource dimension of protected space. All three non-experimental strategies required relatively few resources, while the resource demand of experimental evo-devo can be considerable. The learning time involved in the non-experimental forms of evo-devo research did not substantially delay these research processes and thus did not require a specific time horizon of protected space. However, researchers who just added evo-devo perspectives to their experimental work could encounter difficulties when they tried to publish outside their disciplinary journals, attempted to publish controversial evo-devo concepts or had a strong evo-devo focus as in the following example:

> One thing I saw is that twice I had papers containing more evo-devo, which were not considered at all for the main journal of molecular evolution, *Molecular Biology and Evolution*, which is the best journal of molecular evolution. And two of our articles – which were then published in good journals –, moreover, have not been accepted in

> this journal. They thought that it was not about molecular evolution, because there was a strong developmental axis, which is quite strange from my point of view.

Thus, adding evo-devo perspectives could affect the time horizon of protected space through delays in publication. Overall, however, only experimental evo-devo research required significant levels of protected space, which depended on the three variables that are now discussed.

Disciplinary Background of Researchers

Among our interviewees who conducted dedicated evo-devo experiments, those who came from evolutionary biology had to modify their research to a larger extent than their colleagues from developmental biology (Table 3). Evolutionary biologists who wanted to move to evo-devo research had to learn molecular genetic techniques and embryological methods, which most developmental biologists already knew and only had to adapt to the new evo-devo questions.

> You know, normally as an evolutionary biologist we usually receive a piece of tissue in a tube, and that's all what you see from the animal […] And then we also started to learn some techniques, so we have a collaborator […] [in the UK]. And he is a purely developmental biologist, who is also interested in Evo-Devo, and he helped a lot to learn things, so I have been to his lab about three times or four, to learn new techniques. So I went once to learn basic histology, another time for In situs, and another time for skin culture. So that has been a great help.

* * *

> You need to know how to breed this organism. You must be fully familiar with it, that is you need to know how it develops. Not just in molecular terms but by observing it under the microscope. So, what happens during the development? You need to know its whole development. Then you need to influence this development molecular genetically and you need to know these methods. That's what mainly happens in the lab.

Table 3. Disciplinary Background Affecting the Protected Space Required for Transitions to Evo-Devo.

Disciplinary Background of Researchers Moving to Evo-Devo	Impact on Dimensions of Protected Space	
	Resources	Time horizon
Evolutionary biology	None	Medium
Developmental biology	None	None

The epistemic background could have a significant effect on the amount of newly acquired knowledge required to engage in evo-devo. Evolutionary biologists needed more time to establish the methods necessary for experimental evo-devo, and thus a longer time horizon of protected space.

Type of Organisms Used in Experiments

The choice of organisms to compare had a much stronger impact on necessary protected space than the general disciplinary background of researchers and associated research practices (Table 4). Experimental biologists generally prefer to work with a few organisms about which much knowledge has been accumulated over the last decades, and with which methods are known to work well. However, these so-called model organisms are not necessarily best suited for answering evo-devo questions, not the least because the evolutionary branch on which they are located constrains the choice of organisms they can be compared to. This is why it is often attractive for evo-devo researchers to work with entirely different organisms. However, including new organisms in experimental research often incurs high costs because little is known about them in the beginning, which makes breeding them and conducting experiments with them more difficult and often more risky than the work with model organisms.[4] Compared to the organisms which are well known to researchers and were chosen because they are easy to breed and to use, the organisms best suited for evo-devo research often require more time.

> For some methods [the transfer] worked straight away, others needed five years. In some cases, we had to spend ten years to transfer each method from Caenorhabditis [model organism] to [our evo-devo organism].
>
> * * *
>
> It's also this with evo-devo: you have to adapt to completely different constraints in new sorts of species. So, now we apply ultrasound to our creatures. Here we are, we had to use ultrasound, people never apply ultrasound to their mice! So we do

Table 4. Type of Organisms Affecting the Protected Space Required for Transitions to Evo-Devo.

Type of Organisms Used in Experiments	Impact on Dimensions of Protected Space	
	Resources	Time horizon
Model organisms	None	None
Non-model organisms	high	high

ultrasound on our hedgehogs and on [another non-model organism], to see at which stage embryos are, to be able to take them. Only the breeding of these animals, that took us two years to master the breeding.

* * *

A: And for that we had to develop these three techniques.

Q: Was this complicated to set up and, let's say, expensive?

A: Yeah, it was complicated, because in fact you do it through detours. Because it is a technique that worked very well in the fly but does not in vertebrates for rather complicated reasons. So we had to introduce a kind of molecular scissors in [our vertebrate], tinkering.

Evo-devo researchers who did not work with classical model organisms occasionally had difficulties when attempting to publish their results. They faced criticism because they did not meet the standards of work that had developed for model organisms. The new organisms could not be manipulated the same way as model organisms because the knowledge and tools had not been developed yet. As a consequence, the functional tests that were expected in the field, and particularly from reviewers, could not be conducted with these organisms.

I: And what was the problem in the view of the [journal] reviewers?

The problem that came back to us was that we lacked the ability … We were showing this one gene, a gene that is very famous for all sorts of reasons, to be involved in the very early development of the trait that we were looking at. And the comments that prevented it to making it to higher journals were that we were lacking what we call functional tests in developmental biology, which means the ability in gene in a developing system to see what does it do to the system when you manipulate it. We could see that it was expressed, we could see that it was there before this or that, we could see that it was expressed not in lineages versus not others. What we could not do was manipulate it on the wing to ask the question, okay, when I mess it up, what happens.

* * *

Yes, in fact we have difficulties for some of our evo-devo work. If you go to high profile journals they would come back and say – why didn't you do a functional study? Why haven't you studied how the genes are actually working rather than just seeing if they are expressed? And the answer is – you cannot, but it is still very interesting to find out what you can find out about these organisms. […] And that is not always very much because they are very difficult animals to work on, there are all sorts of technical problems that stop you from doing this very high end technical type of things. But the really big developmental journals they want technical high end papers, in general. So they question some of these things we send in because they do not work with comparative things, they work on model organisms. They do not see the enormous challenges that it presents. You just cannot do it, it is the short answer.

* * *

Q: In terms of publications and related to your switch to Evo-Devo, was it easier or more difficult to publish?

A: No, much more difficult. […] It takes place in a more restrictive setting, as it is more multidisciplinary, where we must satisfy both developmental geneticists and evolutionary biologists. This is a problem to publish the evo-devo [work] because journals are either one or the other, typically. So often we see immediately: 'Oh yes, that's a developmental geneticist [reviewer], he wants functional in every way'. He does not realize that we are working on something other than the mouse. He asks infeasible things. Or he asks, or he criticizes disregarding the fact that we do not work with the mouse. We expect to be told 'wow, it's still fantastic what you did with your animals. So it is not easy ….

Working with new organisms had a strong impact on both the resource and the time dimension of protected space. In particular, the time dimension often became unpredictable due to the necessity of establishing methods for the new organisms and due to delays in publishing. Only a few special evo-devo journals exist so far (McCain, 2010). Although they have an interdisciplinary focus, they have a lower reputation than the established disciplinary journals. This could hinder the advancement of careers and grant applications. At the same time, the epistemic rewards of this strategy are likely to be higher due to the organisms' suitability for evo-devo questions. Introducing new evo-devo-specific model organisms in a laboratory is the 'high risk, high reward' strategy of evo-devo. It requires a larger protected space in both dimensions but is also the potentially most rewarding in terms of scientific yield.[5]

Approach to Comparisons

Another decision of researchers that considerably affected the protected space needed for transitions to evo-devo research concerned the ways in which comparisons between species were conducted (Table 5).

Table 5. Approach to Comparisons Affecting the Protected Space Required for Transitions to Evo-Devo.

Approach to Comparisons		Impact on Dimensions of Protected Space	
Comparative experiments	Organisms from one species	None	None
	Organisms from similar species	Low	Low
	Organisms from dissimilar species	High	High
Experiments compared to data	from the literature	None	None
	from collaborators	Low-medium	Low-medium

Comparisons could either be achieved by carrying out comparative experiments with different organisms in the researcher's laboratory or by experimenting with just one type of organism and using externally produced data for comparisons. The most difficult and thus most resource-intensive and time-consuming way to conduct comparative evo-devo experiments is working with two different organisms in one laboratory. In most cases, this approach to comparative research is more risky and costly because researchers have to establish (introduce, breed and understand) a second organism in their laboratories (non-evo-devo research is mostly conducted with only one organism). The advantage of comparative experiments is that the experiments are designed within the same conceptual and methodological framework, which guarantees the best fit of data.

> One thing is the feeling for the organism in biology, you have to learn, you have to know the local effects. It takes a while before you get to know a [certain plant species], the things that you can do and the things that you cannot do, what is normal, what is abnormal, […] like diseases in the greenhouse. You have to know, it looks like that, you have to treat like that. You don't ever see anything about it in the paper but if they all die because of some disease – that takes so long to learn that. At some point Arabidopsis entered, on the lab floor people hated it because they were not used to it. You have to get used to it and know what you can do with it and what you should not do.

There are several ways to reduce these investments. One approach was to conduct comparative experiments but to use only one species, from which different transgenic individuals are constructed. Since only one species is used, both breeding the organisms and the application of methods are less risky and costly because of the overall similarity of the organisms involved. Our sample included one plant biologist and one zoologist who used this approach. Another way of reducing risks and costs is producing the comparative information internally but using species that are very similar (e.g. two species of fish). Again, breeding and using the second species requires less learning because of the similarities, and the experimental methods are more likely to be easily transferred.

Costs of comparative experimental research can also be reduced when information about the second organism is acquired from external sources rather than internally produced by experimenting with several organisms in one lab. This can be done through collaboration with other evo-devo researchers, who are specialised in the other organisms. An even easier way is to include published data on the organisms or to use bioinformatics databases. However, both collaboration and reliance on literature or databases reduce a researcher's control of the experimental approach and the data that can be used. The data that are accessible this way may not fit the specific evo-devo question, thereby limiting the potential epistemic rewards of these cost-effective strategies.

> Q: But where exactly comes the evolutionary part in?
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> A: It is when there were enough sequences from different species across the whole range to compare them.
>
> Q: How do you do this: You have Arabidopsis, and you have [another plant species]?
>
> A: You look up the databases. You have your gene that you are working with and put it against the whole database. The computer screens it, compares it one by one. This one matches 80%. So you compare the [other plant species] gene to the Arabidopsis gene … Same evolutionary origin, 80% identical.
>
> * * *
>
> Q: You used Drosophila then as a second model organism for comparison […]
>
> A: Well, it was more at the theoretical level because, for obvious reasons, there is much, much more work done in Drosophila than not only in insects but in many other organisms probably. So it was my comparison insect, I was working on a gene called […] and most of the work has been done in Drosophila. Of course, this was my […] reference point at least from the literature, comparison perspective.

This discussion of the four major variables affecting the level of protected space required for different transitions to evo-devo research demonstrated the complexity of research strategies, and the large 'population' of possible evo-devo research tasks. Each of the tasks within this population required specific protected spaces, which in turn implied a specific fit with the 'authority landscape' in which researchers made decisions on tasks and approaches. In order to enable comparisons of authority relations and their impact on the selection of evo-devo research tasks, we now reduce the complexity by identifying three levels of protected spaces that can be linked to particular sets of authority relations.

Three Levels of Required Protected Space

The impact of these four variables on the resources and time horizon dimensions of required protected space can be integrated by distinguishing three levels of necessary protected space, which are linked to the degree to which the specific evo-devo research deviates from established research practices, as summarised in Table 6.

Table 6. Degrees of Protected Space Required by Different Types of Evo-Devo Research.

Degree of Protected Space (in Resource and Time Dimensions)	Types of Transitions to Evo-Devo Research
Large	Setting up comparative experiments with dissimilar species
	Setting up experiments with one non-model organism when coming from an evolutionary biology background
	Organising large collaborative networks for comparisons
Medium	Setting up comparative experiments with organisms from one species or from two similar species
Small	Adding evo-devo perspectives to traditional experiments
	Theoretical or bioinformatics research

1) *Large protected space* was needed when a move to evo-devo included producing the empirical evidence by comparative experiments with two or more dissimilar species. In exceptional cases experiments with only one organism could also require large protected space, e.g. when a non-model organism was established by an evolutionary biologist who moved to evo-devo research and who had to establish a molecular biology lab. The other exception was a researcher who experimented with only one organism and acquired the data about other organisms from collaborators. He compared so many organisms that he had to build a rather large network of collaborators, which in the end was as time-consuming as establishing a second organism in one's own lab.

> […] there were two problems to do experiments in comparative development. One was to get the embryos from all these different species. It has taken me years to build up a big network of collaborators. So I can now get embryos from very rare species quite easily. […]

> With the […] limbs we were working for seven years. Collecting the species, […], cloning the genes, waiting for a new species to come in. Comparative studies take a long, long, long time.

Researchers who kept several different species in their laboratories needed breeding facilities (e.g. animal houses) for these different species, including technical support. Manipulating additional and particularly non-model organisms in the lab also required a longer time horizon. Molecular genetic tools needed to be adapted to non-model organisms, particular those that were unique even to the evo-devo community. Due to the lack of genetic tools, the work with certain species is technically very difficult and hence very time consuming. Obtaining sufficient embryos from certain species required a high amount of time because mating does not occur every year.

2) *Medium protected space* was required for evo-devo research that experimented with only one species and acquired the empirical evidence about the other(s) through collaborations, from the literature, or from databases of gene sequences. The necessary protected space was also medium for evolutionary biologists who added only a small 'devo part' to their work, e.g. by investigating the function of single genes. Another approach to limiting the costs of comparisons was conducting within-species comparisons, which required the application/development of genetic tools for only one species, or working with species that were similar enough not to incur additional costs for breeding and adapting genetic techniques.

   Researchers who worked on only one organism nevertheless needed time to adapt genetic tools for manipulation if this organism was a non-model organism. This was even impossible in some cases, which led to publication difficulties. This is why the necessary protected space is medium in both the resource and time dimensions.

3) *Small protected space* was required by all evo-devo research that was non-experimental, either because it just added the evo-devo conceptual perspective to the interpretation of traditional results or because it was theoretical or bioinformatics research. The transition to evo-devo could be achieved by continuing one's work largely unchanged and additionally framing experimental results in an evo-devo context. The protected space required by the experiments was necessary for the non-evo-devo research, i.e. for common experimental research in the field. The actual transition to evo-devo did not require additional resources or time. Publishing results could also be continued in the researcher's main field. The necessary protected space was also low for all researchers who developed theoretical concepts in evo-devo (e.g. certain hypotheses), or used bioinformatics data for answering evo-devo questions. In both cases, costly experiments are unnecessary.

THE IMPACT OF AUTHORITY RELATIONS ON PATHS TO EVO-DEVO

With our empirical basis we could test numerous situations of evo-devo transitions (requiring low, medium or high levels of protected space) in four national constellations of authority relations. This enables us to determine necessary and facilitating conditions for evo-devo research and how they are met. Further we can specify who is actually able to build the necessary protected space in the four countries and why.

Ecological Niches for Evo-Devo Research Provided by Different Sets of Authority Relations

Having identified three types of protected space that can be linked to most of the research tasks formulated by evo-devo researchers, we can now ask how different sets of authority relations created niches for researchers in which these protected spaces could be built. We do this by identifying necessary and facilitating conditions for building protected space and the authoritative agencies involved in creating these conditions (Table 7).

The most general condition for evo-devo research to be possible at all is that scientific communities accept the outcomes of evo-devo research as contributions to scientific knowledge. As we have seen in the discussion of publication problems, this condition is not always fulfilled because evo-devo experiments can have difficulties in meeting the standards set by researchers on traditional model organisms. These affected researchers' choices, particularly those of researchers who still had to advance their careers.

For a transition to evo-devo to be possible in any national science system, this type of research had to be deemed worth supporting by the authoritative agencies that provide positions and resources to researchers. Some properties of evo-devo research turned out to be particularly important:

- Evo-devo research is basic research for which applications (be they medical or agricultural) cannot be convincingly promised.
- The research on which evo-devo conceptual extensions (evo-devo perspectives) build also is basic research with no applications in sight.
- Evo-devo research is non-mainstream interdisciplinary research that risks less recognition and delayed publication of results.

These properties may be at odds with political or managerial preferences for contributions to societal ends and with national and organisational evaluation systems. This is why the actual fit of basic research in general and evo-devo research in particular with the interests of research organisations (universities and public research institutes) is a necessary condition for all three types of evo-devo research. Therefore, the three conditions are necessary for all evo-devo research to be undertaken are: (1) evo-devo results

Table 7. Necessary and Facilitating Conditions for Building Protected Space for Evo-Devo Research.

Conditions for Evo-Devo Research	Protected Space		
	Large	Medium	Small
	Resources for breeding facilities and large groups, long time horizons	Resources for evo-devo experimental projects, sometimes unpredictable time horizons	Resources for theoretical or experimental research
Acceptance by scientific communities of evo-devo results as scientific contributions	Necessary condition	Necessary condition	Necessary condition
Acceptance of basic research by the research organisation	Necessary condition	Necessary condition	Necessary condition
Acceptance of evo-devo research by the research organisation	Necessary condition	Necessary condition	Necessary condition
Project funding for basic research	Necessary condition	Necessary condition	Necessary for evo-devo conceptual extension of experimental research, facilitating for other
Control of infrastructure	Necessary condition	Necessary condition	Necessary for evo-devo conceptual extension of experimental research, facilitating for other
Above-average investment in infrastructure	Necessary condition	Facilitating condition	Indifferent
Tenured position	Necessary condition	Facilitating condition	Indifferent
Project funding for interdisciplinary collaborations	Facilitating condition	Facilitating condition	Indifferent

must be accepted by the scientific communities as scientific contribution, (2) Basic research must be accepted by the research organisation, (3) evo-devo research must be accepted by the research organisation, as summarised in Table 7.

Beyond these three necessary conditions other conditions vary in their implications for developing different levels of protected space. Project funding for basic research is a necessary condition for most experimental research, making theoretical evo-devo research and the research working with databases the only forms of evo-devo research that can be undertaken without such project funding. Experimental research in the biosciences additionally requires control of infrastructure in the form of a laboratory and the basic equipment that comes with it. The crucial step of experimental evo-devo research is establishing the different species as experimental objects. This includes building the infrastructure for breeding the species and developing the molecular genetic techniques that are necessary to modify the organisms. In other words, an evo-devo laboratory has to be established.

This infrastructure is commonly provided by universities. Providing high levels of protected space involves above-average investments in infrastructure. A dedicated evo-devo-lab is large and often depends on expensive breeding facilities for more than one species. Research organisations must be able and willing to make these investments.

The medium-sized protected spaces for evo-devo research do not depend on above-average investments. However, since they are linked to dedicated evo-devo research questions, additional investments might be necessary if new species are to be bred. Such evo-devo research will be facilitated by investments in the additional infrastructure requirements.

The long and – more importantly – often unpredictable time horizons of large and medium-sized protected space for evo-devo research made a tenured position important for most researchers. While they were necessary for research requiring large protected space, we did observe transitions to evo-devo research that required medium-sized protected space by researchers in fixed-term posts. Some laboratories specifically recruited postdocs with evo-devo experience in order to expand this line of research. However, the time horizon provided by fixed-term positions was not always sufficient. One researcher postponed a more 'hard-core' approach of evo-devo because the labour-intensive developmental genetics work would have extended beyond the duration of his position. Finally, researchers relying on collaborations for the comparisons between species benefited from project support for interdisciplinary collaborations.

Who Could Build Protected Space in the Four Countries?

Having identified the necessary and facilitating conditions for building protected space and the authoritative agencies controlling these conditions, we can now ascertain how protected space could be built in the four countries. The discussion of conditions in the previous section already indicated that opportunities strongly depended on researchers' career positions, and that there may be functionally equivalent ways of providing the other conditions. This is why the following discussion is focused on the three types of protected space, and the ways in which conditions for building these spaces in the different countries are compared.

The building of *large protected spaces* was the most demanding task because it depended on simultaneous and sometimes coordinated support of all authoritative agencies. Acceptance of evo-devo research by scientific communities is a condition on the international level, which existed for all of our four countries to the same extent. In the mid-90ies, support for basic research and particularly of the kind of basic research represented by evo-devo was available, and led to initiatives for evo-devo to be established in two of the smaller countries, Sweden and the Netherlands. The third small country, Switzerland, had a strong research tradition in the relevant biosciences and has actively contributed to the development of evo-devo, while the larger German science system also hosted a strong tradition in these fields. Support for evo-devo included project funding for the basic research on which evo-devo builds and for evo-devo research itself. In all four countries, this depended on national and international funding agencies providing project funding for basic research, i.e. on the research councils[6] which represented state interests.

> I had from the start the opportunity to acquire external grants. And it always worked. It is not particularly easy in the evo-devo area because it is not medical, applied research. It is always easier to get money for those areas because there are predefined research priorities for which you can apply directly. We do not fit in these. We always have to apply for programmes that provide complete freedom content-wise. That is traditionally the DFG Individual Grants Programme. This always worked if it was a good evo-devo project. (German researcher)

We found a few exceptions from the need for gaining grants. In German state-funded non-university research institutes and at one Swiss university researchers had sufficient recurrent funding to immediately start evo-devo research without being dependent on external grants.

The fate of evo-devo in the Netherlands demonstrates, however, that the support for evo-devo research by the state, research organisations and funding agencies cannot be taken for granted anymore. The state has recently formulated strong political expectations concerning the utility of university research, and has specified these conditions by defining priority fields. Universities are expected to include these fields in their research profiles, and are financially rewarded for doing so. Funding agencies are confronted by similar expectations and follow them.

> The money for evo-devo has dried up, and it is really difficult to get funding, unless it has an applied aspect. So I moved a lot more recently into … [a biomedical direction]. So I still do a bit of evo-devo, […]. And we can use it as an assay. But pure evo-devo is kind of on the way out I think. Because it is fundamental research, and all the funding is shifting, well a part of funding is shifting to clearly applied research. (Dutch researcher)

Dutch universities responded to state expectations by discouraging the kind of basic research represented by evo-devo and the fields on which it builds and increasing their demands for research that is connected to applications. Biologists in the Netherlands are increasingly expected to show potential biomedical or agricultural applications, an expectation that usually cannot be met by evo-devo researchers. Universities ceased to invest in groups that cannot meet these expectations. One evolutionary biology group was closed, and several biology chairs were re-dedicated towards more application-oriented research.

Since publications in high-impact journals were an important promotion criteria and a requirement for grant applications, one researcher moved away from evo-devo research.

> I tried writing a [grant] two years ago for the evo-devo stuff. And I didn't get [it]. And probably next year I will write a [grant] about […] development, simply because we have now two publications in the pipeline with this group and they will go to big journals and they will be cited. Simply your chances are much bigger. And career-wise, being on a tenure track and people looking at your H-index and whatever it is these days – you feel like you have to make those kind of choices rather than risking doing it again and getting rejected again. (Dutch researcher)

The worsening climate for basic research let several evo-devo researchers leave and taking up offers abroad. As a consequence of these developments, evo-devo research in NL has almost disappeared (see Laudel & Weyer, this volume).

The control of infrastructure that was necessary for building large protected space was limited to professors or – in Germany – directors at state-funded public research institutes. Professors could build evo-devo labs from start-up packages they received with their appointments. In Switzerland, Sweden and the Netherlands evo-devo researchers were actively recruited with the offer of establishing an evo-devo lab. However, high levels of protected space depended on above-average investments. In our sample, only Swiss universities were affluent enough to support local research interests that required such investments (see Benninghoff et al., this volume). The strong research tradition in developmental biology and in evo-devo (Swiss researchers contributed to some of the early discoveries that set the field in motion) created enough interest in some universities to make them invest in the required infrastructure. In Germany, investments of this kind were made in state-funded public research institutes rather than universities. Although the biosciences are strong enough for interest in evo-devo to emerge in many German universities, the latter's capacity for above-average investments is limited (on the comparison of universities and public research institutes see Gläser et al. in this volume). The case of Sweden demonstrates that exceptionally large grants could provide a functional equivalent to university funding in infrastructure. One of the Swedish funding agencies intended to promote evo-devo research.

> The VR [Research Council] had decided to push for funding for a professorship in evolutionary biology at the border between traditional and modern molecular evolutionary biology. And that had then been set for some sort of competition among universities in Sweden and it was Uppsala who had won it. And [...] there were all sorts of different candidates with different profiles that were interviewed. But several [...] had probably some sort evo-devo perspective, or at least some kind of combination of historical data with molecular data. (Swedish researcher)

In this case, the majority of the funding came from the grant, with some matching funds contributed by the university.

The long or at least unpredictable time horizons of large protected space for evo-devo research made tenured positions important. Since these had to be combined with the control of infrastructure, most researchers who built large protected spaces had professorial posts and headed evo-devo laboratories. Only one Swiss and one German researcher on temporary positions attempted evo-devo research that required large protected space. The Swiss researcher could utilise the large protected space created by the professor, but within the limits of the lab (particularly the animals established there). The German researcher worked as a group leader at a state-funded institute in which evo-devo research was firmly established and which provided excellent facilities as well as extraordinary technical support. He had discretion over several PhD students and divided his research into a risky evo-devo line requiring large protected space and a low-risk research line that secured publishable results.

Medium levels of protected space could be built without above-average investments in infrastructure. This was possible in all four countries for researchers who could establish an evo-devo lab and had access to project grants. Tenured positions were an advantage due to the sometimes unpredictable time horizons, which is reflected by the fact that Dutch researchers on tenured positions below the professorial level built medium-sized protected space. Researchers on fixed-term positions could build medium-sized protected space when working in an evo-devo lab but faced the restrictions described above.

Low levels of protected space were easiest to build. In the case of conceptual extension, however, it was small only for the evo-devo part of the research, while the foundations of disciplinary experimental research in the biosciences still had to be provided. For these small protected spaces to be built, basic research had to be tolerated by universities and had to be able to attract some grant funding.

The low threshold for entering some forms of evo-devo research and the opportunities to develop it gradually without having to give up previous lines of research suggest that some kind of evo-devo research is possible everywhere. While this is true to a limited extent, career expectations of prospective evo-devo researchers affected their decisions. For young researchers, the opportunity to build a career with evo-devo research was very important. Evo-devo research or the basic research it builds on had to be able to attract funding, and results had to be published. For researchers still having to meet criteria for tenure, avoiding evo-devo research was the safest option, which was chosen by two Dutch researchers.

The existence of large evo-devo labs and the many opportunities for ‘low-threshold transitions’ made the move to evo-devo research possible for researchers at all career stages. Laboratories whose leaders were interested in evo-devo without wanting to move to it themselves offered opportunities for postdocs to begin evo-devo research. The dedicated evo-devo laboratories also provided the necessary protected space for younger researchers, who in many cases specifically sought employment in an evo-devo lab in order to move into that field.

Under these conditions, it was quite common for researchers who became interested in evo-devo to start with topics that required small protected space (e.g. theoretical evo-devo or adding evo-devo perspectives to traditional experiments). Researchers thus could explore the potential of evo-devo ideas as well as publication opportunities without risking too much, because their experiments still 'counted' in the traditional context. If things went wrong, it was only the 'add-on' that failed, while the basis of experimental research still provided publication opportunities and access to grants. If they were successful, they moved to evo-devo that required medium-sized or large protected space. One developmental biologist had started with theoretical evo-devo work. He first added to his classical developmental experimental research conceptual considerations on evo-devo. Then he moved to do theoretical evo-devo research, using literature data. Finally he set up an evo-devo lab and started to do evo-devo experiments.

> A: I switched really from classical evo-devo to much more molecular stuff. Now I'm looking at the old theoretical papers I did on evo-devo and now say, let's re-address this work with molecular tools.
>
> Q: And classical would be just looking at the morphology?
>
> A: Morphology. All the literature, historical aspects, theoretical aspects. Now it is much more experimental, molecular.

An evolutionary biologist began his evo-devo research in the early 1990s, i.e. at a time when the methodological development of evo-devo methods were still at its early stages. He published an article that was purely theoretical.

> A: [...] That was the argument I put forward in this article without any empirical evidence whatsoever, looking at the morphology. [...] It also reveals so to speak the gap between conceptual insight and technical ability. I mean, it is possible to write something like that as soon as you have the idea, but to actually do something [empirically] took time.

This work required only very small protected space. The transition to evo-devo benefited from collaborations, which supported the researcher's learning. The researcher later acquired his own evo-devo lab and eventually built large protected space for evo-devo research.

The specific nature of evo-devo research as a scientific innovation that not only leads to new experiments but also combines and overlays traditional experimental research made it possible and often easy to add evo-devo to already existing lines of research, and to move to the new research only partially. This is trivial for all cases in which traditional experimental results were just interpreted in evo-devo theoretical contexts but also applied to those researchers who built medium-sized and large protected spaces. Only one Swiss, two Dutch and one German researcher of those that we interviewed changed their research completely and conducted only evo-devo research in the end.

CONCLUSIONS

If we stay in the vocabulary of our biologists, evo-devo research has proven to be a highly adaptable species. The variability of research tasks contributing to the progress of the new field made the field as a whole highly adaptable to variations in research traditions and authority relations. In spite of this variability, however, both individual strategies for building protected space and the development of evo-devo at national and international levels depended on particular sets of authority relations. General conclusions about this dependency can be drawn as follows.

The most fundamental condition is the acceptance by scientific communities of the legitimacy of the innovation. To be a researcher means producing contributions to the knowledge of one's scientific community, which has exclusive authority over this definition. This authority has been increased by changes in the governance of science because new evaluation procedures also channel it through grant funding, organisational evaluations, and individual evaluations for recruitment and promotion purposes.

An important condition at the national level is the acceptance of research of the evo-devo type – purely basic, non-mainstream, low-impact – by national authoritative agencies. These include the state, national elites, funding agencies, research organisations, and organisational elites. The Dutch case shows how the new public management reforms and the increasing incorporation of public policy goals in science policies can lead to a situation where all these authoritative agencies become 'aligned', and research that does not fit state expectations be crowded out. This applies to both evo-devo research itself and the fields of evolutionary and developmental biology it depends upon.

Third, while some forms of evo-devo research might be possible even under the worst conditions, evo-devo as a field can only progress if medium-sized and large levels of protected space can also be built. Researchers usually plan some years ahead when formulating research tasks, which means that it must appear possible to them to make a career with evo-devo, which in turn requires moving from positions in which small protected spaces can be built to those that enable the building of larger ones.

Fourth, the large protected spaces required by 'true' evo-devo research – experimental comparisons of unusual organisms within one lab – highlighted yet another necessary feature of authority relations. Large protected space can only be created if authoritative agencies set priorities – either because they want evo-devo research or because they want specific researchers and accept that they have to create the infrastructure in order to attract the researchers. However, not all research organisations appear to be able to support these investments. German public research institutes, Swiss universities and a Swedish funding agency were able to create these niches, as was a 'joint venture' of a Dutch funding agency and a university. The fact that these particular sets of authority relations all deviate from those commonly available at the contemporary average European university indicates that the general shift from block funding for research to external project grant funding might have overshot its target, and now unduly limits the authority of universities.

Finally, the fate of evo-devo research in the Netherlands points to the danger of an international homogenisation of authority relations. The changes in authority relations that endangered evo-devo research in the Netherlands occur in many countries. If the trend towards a homogenisation of state interests, thematic priorities for research and intrusive, short term governance instruments persists, research of the 'evo-devo-type' might be crowded out in the future. Scientific research appear to thrive under conditions of institutional diversity because research tasks will be formulated where the necessary protected space can be built. It doesn't matter to international scientific communities which country provides the conditions. If, however, no country at all provides opportunities to build specific protected spaces, some kinds of research might disappear or at least slowed down considerably.

NOTES

1. See Mullins (1972) on the Phage group and the genesis of molecular biology, Edge and Mulkay (1976) on the emergence of radio astronomy in Britain, Ben-David and Collins (1966) on Psychology, Dolby (1976) on physical chemistry, Law (1976) on X-ray Protein Crystallography, Mullins (1973) on ethnomethodology, Fisher (1966/1967) on the theory of invariants. Chubin (1976) published a critical review of the research on the emergence of scientific specialties. Two anomalous fields have also been studied. The field of 'N-rays' died relatively quickly (Nye, 1980), while the cold fusion lived on for quite some time (Lewenstein, 1992, 1995; Simon, 1999).

2. Thus, we do not apply the concept 'scientific innovation' to all findings that are accepted and adopted by other researchers (as does Knorr-Cetina, 1981, p. 66)

but limit it to findings that have implications for a whole scientific community such as Lynch and Jordan's example of a biological innovation (the polymerase chain reaction) shows (Lynch & Jordan, 2000).

3. Interview quotes in German, Swedish and French were translated by us.

4. In some cases, these difficulties motivated the selection of species similar to those of established model organisms, which made breeding and manipulating them easier and increased the likelihood that methods could be successfully transferred.

5. In recent years evo-devo has been developing its own model organisms. Thus, analytical toolkits become available to manipulate those organisms (Sommer, 2009). However, most of our interviewees didn't have this advantage yet when they moved to evo-devo research. Therefore the time period of a researcher's transition to evo-devo is important in terms of transition costs.

6. The *Deutsche Forschungsgemeinschaft* (DFG) in Germany; The *Schweizerische Nationalfonds* (SNF) in Switzerland; the *Nederlandse Organisatie voor Wetenschappelijk Onderzoek* (NWO) in the Netherlands; and the *Vetenskapsrådet* (VR) in Sweden.

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