Adadptation, organisms, individuals: about some conceptual issues.

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- The main question: how does evolutionary transition research impact on our conception of adaptation and organisms?

Outline

- Organisms, adaptation, individuality: the classical darwinian view and problems
- The evolutionary transition programs, a new take on individuals
- The new ridddle of adaptation. An hypothesised solution
- Consequences about individuality

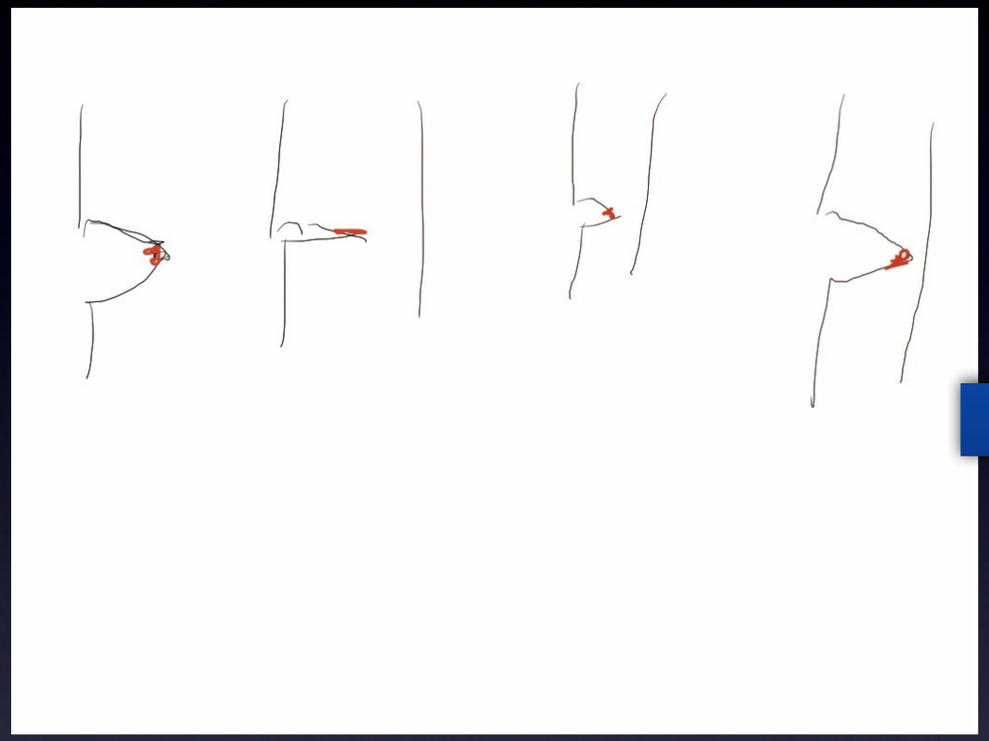
- **Organisms, adaptation, individuality: the classical darwinian view and problems**

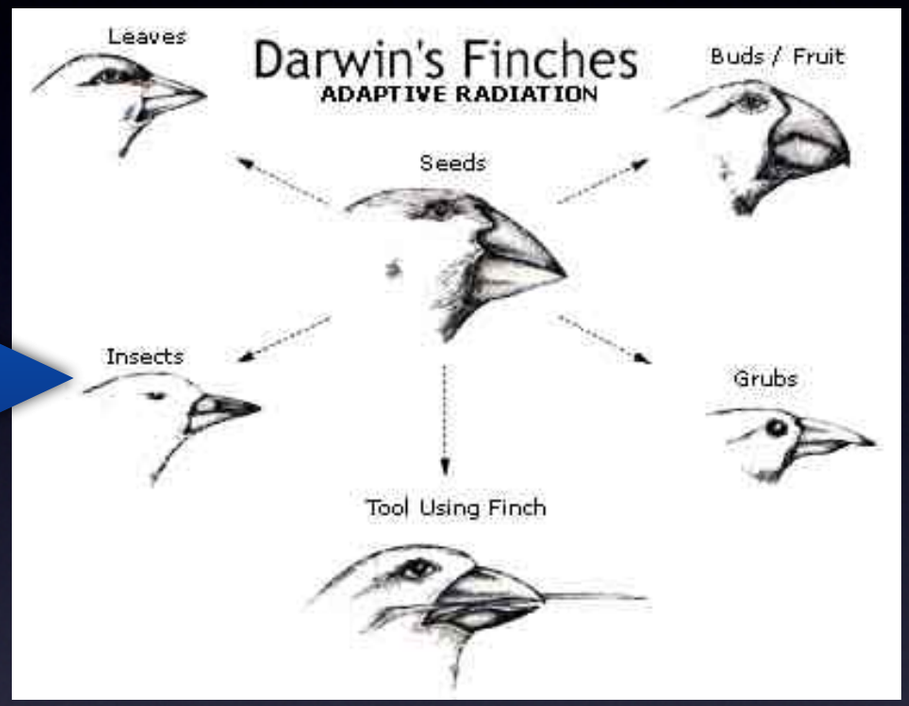
The Darwinian framework

Adaptation

- **Adaptation**: natural selection explains the fit between organisms and their environment.

- (Finches)




Darwin's Finches
ADAPTIVE RADIATION
Leaves
Buds / Fruit
Seeds
Insects
Grubs
Tool Using Finch

- **Traits** are adaptations in the first place:

  - By Darwin himself: "natural selection acts by **either now adapting the varying parts** of each being to its organic and inorganic conditions of life; or by having adapted them during long-past periods of time: **the adaptations being aided in some cases** by use and disuse, being slightly affected by the direct action of the external conditions of life, and being in all cases subjected to the several laws of growth". (Darwin 1859, Ch 6)

  - This is reinforced by the Modern Synthesis, via the focus on genes as determinants of heritable traits.

Organisms

- Entities with design, showing "exquisite contrivances" (Darwin): functional integrity and organisation

- Tension between: "organisms are adapted" / "traits are adaptations".

  - Solution: organisms are "bundles of adaptations" (Huxley 1942)

    - Idea of " trade-off adaptationism": organisms instantiate a trade off between adaptations for distinct environemental demands

- Target of the Gould-Lewontin attack on adaptationism (idea of "*Bauplan*" as a set of constraints initially imposed onto adaptions)

- Modern Synthesis= "eclipse of organisms" (Fox-Keller 2001)

- Due to the central position of **population genetics** as the science of the process of evolution by natural selection. (see also Gould, "hardening" of the Synthesis)

- Many challenges to MS target this (Bateson 2005)

Huneman, "Assessing the prospects for a retun of organisms", *History and philosophy of life sciences*, 2010

Individuals

- "*Individuals*" in general: cohesion between parts, disappear when added or divided

- Organisms were for a long time the *paradigm of individuality* (Aristotle, Leibniz, etc. in metaphysics; ordinary biological talk)

    - Individuals are often identified by *analogy* with organisms (the "beehive" analogy in the 18th century-> the "superorganism" in Clements ecology, 1920)

        - But *some individuals* seem to be very different than metazoan organisms : portuguese men of war, fields of dandelions, slime molds sometimes... (e.g. lack of spatial or temporal cohesiveness)

- Evolutionary theory provides a criterion of individuality : being a unit of selection. (Hull, 1989).

- Various levels of selection (Brandon, 1989; Gould and Lloyd, 1990, etc.) make for many kinds of individuals.

- **The evolutionary transition programs, a new take on individuals**

The evolutionary transitions program

- Focus: transitions in individuality
- Switch the question: not "*what are* the individuals?" but "how did the kinds of individuals we know *come to exist*?"

- Classical Modern Synthesis frame *assumes* the units of selection (genes, organisms, etc.). But they are themselves *resulting* from ENS.
    - This switch impacts our conception of selection itself (Griesemer 2000)

- In general, dropping the assumption that units of selection are given entails rethinking crucial notions:
    - Selection (Griesemer 2000)
    - Inheritance (Maynard Smith and Szathmary: limited vs illimited heredity)
    - Fitness
    - Information (Maynard Smith and Szathmary: new individuals = new ways of storing information)
    - Adaptation

- Consequence: (against the idea of "eclispe of organisms") from the viewpoint of Darwinian theory, one tries to explain the ***fact of multicellular organism (***ie: why do living things mostly come now under the form of multicellular organisms?)

- Huneman, "Assessing the prospects for a retun of organisms", *History and philosophy of life sciences*, 2010

How actually explanations (e.g. Buss 1987)
How possibly explanations

- Two general ideas:

- What now are individuals were once groups of individuals living on their own ---> how has / how could selection lead these free-living individuals to come together?

    - Hence, *multilelevel selection* is a privileged explanatory scheme (e.g. Michod 1999)

- The threshold of individuality is reached when groups reproduce as a whole.

("Entities that were capable of independent replication before the transition can only replicate as parts of a larger unit after it" (Maynard-Smith and szathmary 1995, p. 227).

Evolution of individuality: a two-stage process

- A. A first stage: model the conditions under which evolution by natural selection works in a way that favors tradeoffs between fitness of entities, so that **socioclusters**—clusters of individuals likely to undergo a common fate—emerge.

- B. second stage: model the way such socioclusters evolve the means to be maintained through time, regularly behaving as coherent wholes because they **get buffered against the higher payoff** to defection

    - first stage : origin question.

    - second stage : maintenance question about high-level individuals. Specific *adaptations* allow buffering against dismanyling.

Stage 1. “During the emergence of a new unit, population structure, local diffusion in space (Ferrière & Michod 2000) and self-structuring in space (Boerlijst & Hogeweg 1991) may facilitate the trend toward a higher level of organization”(Michod 1999)

Stage 2: "The trend toward a higher level of organization . . . culminat[es] **in an adaptation that legitimizes the new unit once and for all. Examples of such adaptations include the cell membrane in** the case of the transitions from genes to groups of cooperating genes, or . . . the germ-line or self-policing functions, in the case of the transitions from cells to groups of cooperating cells, that is, multicellular organisms. (Michod 1999, p. 42)

The riddle of adaptations in transitions

- The question: in stage 2, these **I-adaptations** *create a new individual*, since they make it unlikely to regress to a group form.
    - But originally, according to the classical meaning, adaptations are traits, hence they *logically presuppose* an individual who carry them.
    - What is the **bearer of such adatations?**

- **The new ridddle of adaptation. An hypothesised solution**

- *<u>Two Usual conceptions of adaptations:</u>*

- **Historical** (Sober 1984, Brandon 1990, etc.) : to be an adaptation is to have come to existence (and remain there) *via natural selection.*

(adaptation statements are historical statements)

- But not all reasons for knowing that X is an adaptation are historical

- Therefore:

- **Currentist view** (Reeve and Sherman 1993) : to be an adaptation is to be *the highest fitness phenotypic variant*.

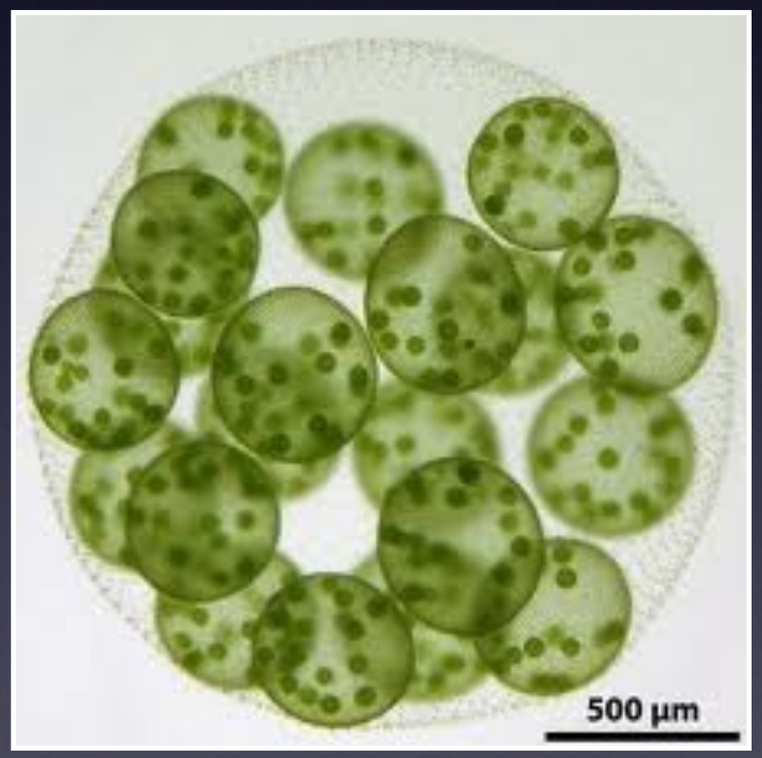
A pluralist interpretation of this duality (Reeve and Sherman 1993, 2001, Brandon 2012)

- Historical view: origin enquiry
- Currentist view: maintenance enquiry

But these views do not fit the adaptations in transitions.

- As a maintenance question, is an I-adaptation an adaptation in the *currentist* sense?
  - Of the "basic individuals" ? But among these the highest fitness individuals precisely don't have the I-adaptation

    (e.g. Hochberg et al 2008, dipersing cheaters...)



  - Of the "high level individuals"?? But then, they are not *variants, since logically there may be only one of these*

- Can it be adaptation in the *historical* sense?
    - saying that the membrane is a result of selection means that cells having and cells not having the property of a membrane were previously competing, and that the “membraned” cells got selected. However, no such selective processes occurred, because any cell already presupposes membranes.
    - Saying that the I-adaptation (eg, cell membrane) is selected as an extended phenotype of low level individuals raises an issue about the beneficiary of this adaptation (the membrane may decrease replication for highest fitness genes..)

Solving the puzzle

- Turning to **inclusive fitness**
- W (a) = direct fitness benefirs + indirect fitness benefits * relatedness
    - Relatedness is understood as *statistical association on the focal locus* (not genome wide association). Hence it can be produced by kinship, *but not only*. (West et al. 2007, "broad kin selection")
        - E.g. Greenbeard mechanism also promote altruistic traits (namely, traits enhancing socioclusters) without relying on kinship. (even if they are more likely in unicellular organisms, eukaryotes, etc.. Gardner and West 2011).
            - One instance of greenbeard has been found playing a role in the transition of slime molds to multicellular life (Queller, Ponte, Bozarro, & Strassmann 2003)
    - Because of the equivalence between kin selection and multilevel selection frameworks (Frank, 2003, West et al., 2007) the multilevel selection schemes can be translated into broad kin selection explanation.

In a population of a species divided in
groups; the more the intergroup competition increases relative to intragroup competition, the more MLS you have for pro-social (altruistic) traits. ->
the between-group variance overcomes the intragroup variance ->
relatedness increases in each set of individuals interacting with a focal individual,
and then in general, which in the end means that kin selection gets stronger,

- In the context of evo transitions, inclusive fitness could be thought as a property of basic individuals (genes, chromosomes, organisms, etc.), not only of organisms; at each level of the transition, they can be ascribed inclusive fitness.

- Here: **what is an I-adaptation?**
- It is the highest *inclusive fitness* variant trait.

Example: apoptosis in cells as a I-adaptation. (Durand et al. 2011)

imagining that one cell mutates into an apoptosis-likely cell: it may reduce its life expectancy, but at the same time, because it creates new opportunities for the cell to which it is related, it gains indirect benefits which can overcome the loss of direct benefit. (Reece, Pollitt, Colegrave, and Gardner 2011)

Therefore, the highest *inclusive fitness is* for the cells likely to undergo apoptosis even against their own survival value, and then the apoptosis can be considered as an adaptation in the currentist sense, to the benefit of those apoptotic cells.

Generally: in a transition process *I-adaptations are traits providing highest inclusive fitness to basic individuals*

About adaptation.

- I-adaptations are cases where the component of indirect benefit is crucial.
    - But given that now the basic individuals benefit from the adaptation (in terms of inclusive fitness), they *can also be seen as adaptations* in the "historical" sense.
        - Depending upon whether the I-adaptation is understood in a maintenance question or in an origin question, the notion of adaptation conveyed will be different.
            - This difference relies utlimately on **timescale differences**: maintenance belongs to **short** time scales and origin to **longer** timescales.

Consequences about individuality.

Consequences about individuals.

- Because kinship is not the only cause for high relatedness, this model of transitions can be extended to some "egalitarian" (Queller) transitions.

Foster et al. 2007: "complete" vs. "component" tragedies of the commons.

- A fourfold distinction between transitions, according to egalitarian/ fraternal,and then the *amount and order of I-adaptations* added to the socioclustering process (complete/ component transitions)

The Four Kinds of Transitions

	Complete transition	Component transition
Fraternal	Transition toward multicellular organisms	Colony of *Melipona* bees (high level of potential conflict makes them different from organisms; see Queller & Strassmann 2009) *Bacillus subtilis* bacteria
Egalitarian	Transition toward eukaryotic cells (mitochondria as symbionts) Termite mounds Macrotermes (Turner 2000) Lichens	Some fig-pollinator wasp mutualisms

- Component transitions : Bacillus subtilis, in which socioclustering occurs, since these bacteria can form a single cohesive individual under conditions of rarefied resources: “Evidently, great populations of single swim-ming cells . . . [use] hydrodynamic interactions to accomplish jointly the tasks necessary for survival” (Solari, Kessler, & Goldstein 2007). But no I-adaptations ensures that this compound will go on reproducing as one piece.

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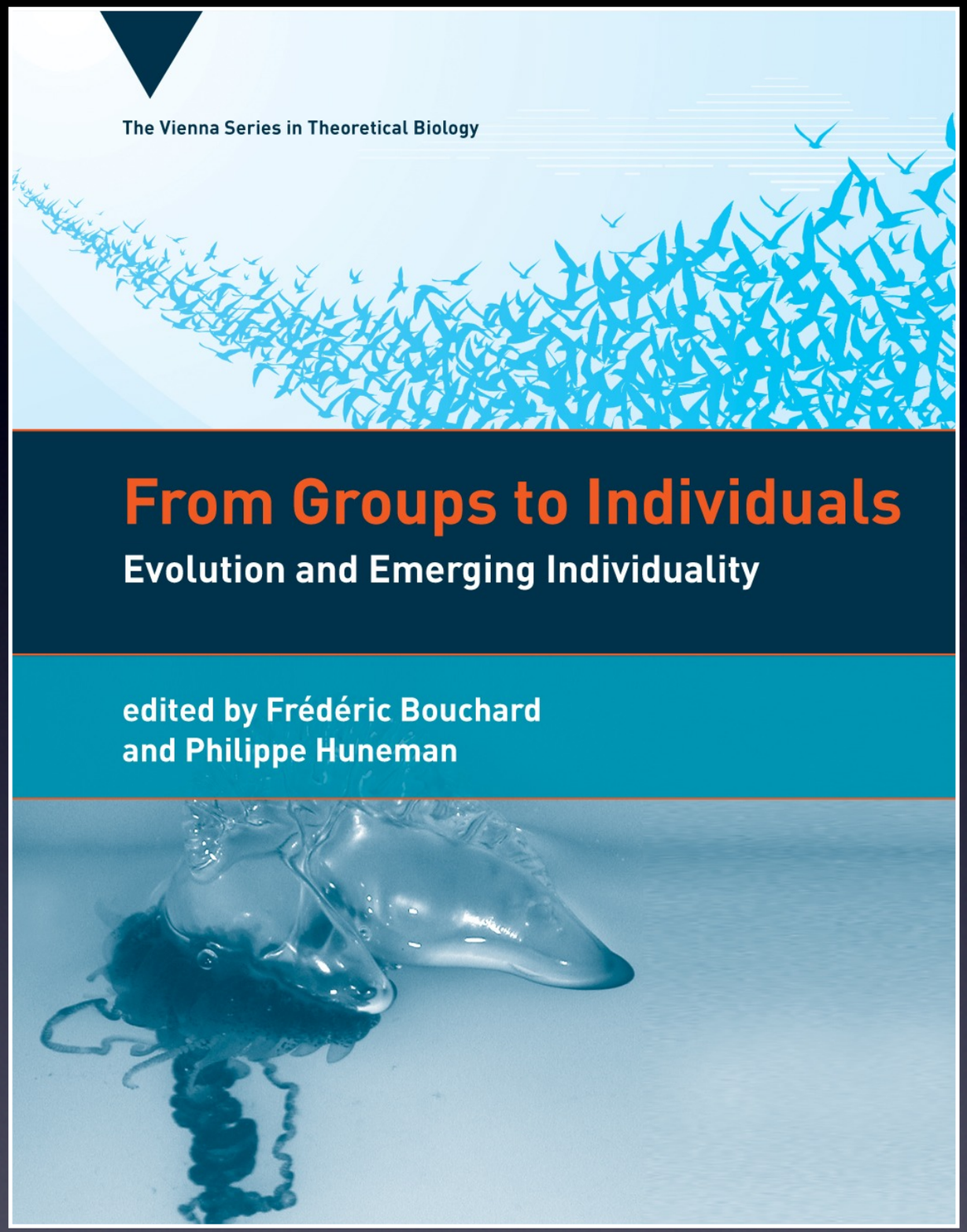
- Therefore: degrees of individuality are evolutionarily understood according to the character of the transitions.

- Since it's not a unilinear scale (but a table) not all degrees of individuality can be totally ordered

- So, not only individuality comes by degrees, but some forms of individuality are not comparable.

- There are many transient individuals.

> “Evolution does not work by major transitions alone. If evolution occasionally crafts new organismal alliances that are truly transformational, it seems likely that it will much more frequently craft new organismal alliances that are not necessarily revolutionary in the history of life, but organismal nevertheless. And if we want to understand the evolution of organismality, we should pay attention to the examples that are recent, to the ones that are unconventional and even to the ones that are incomplete.” (Queller & Strassman 2009, p. 3151)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