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## Emergent properties from organisms to ecosystems: towards a realistic approach

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1 **Emergent properties from organisms to ecosystems: towards a**  
2 **realistic approach**

3

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9

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11

12 **ABSTRACT**

13

14 More realistic approaches are needed to understand the complexity of ecological  
15 systems. Emergent properties of real systems can be used as a basis for a new,  
16 neither reductionist nor holistic, approach. Three systems, termed here BUBBLES,  
17 WAVES and CRYSTALS, have been identified as exhibiting emergent properties.  
18 They are non-hierarchical assemblages of individual components, with amplification  
19 and connectedness being two main principles that govern their build-up,  
20 maintenance and mutual relationships. Examples from various fields of biological and  
21 ecological science are referred to, ranging from individual organisms to landscapes.

22

23 *Key words:* emergent properties, ecological systems, amplification, connectedness.

24

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11

12 **I. INTRODUCTION**

13

14 The concept of emergence was coined to designate properties of groups that cannot  
15 be entirely explained by their individual components (Mayr, 1982). Another meaning  
16 of emergence, not used herein, is the appearance of novelty, for instance the  
17 emergence of life in the universe (Henle, 1942). From a mechanistic point of view,  
18 basic to the emergence of properties that overwhelm those of individual components  
19 is the requirement for individual components to share common properties and for  
20 enough matter and energy to be concentrated in space and time in order to exert a  
21 measurable and long-lasting effect. This occurs through amplification of space- or  
22 time-restricted phenomena, thus passing in a given time and in a given space from  
23 chaos to order (Holland, 1998; Levin, 2000). An example of such amplification of  
24 small-scale processes into macro-scale processes can be easily found in infectious  
25 diseases and, more generally, in non-linear phenomena. In the case of infection, the

1 disease is the emergent property, the microbe the agent, acting at the scale of  
2 individual cells of the host. The disease occurs only once a given threshold of  
3 pathogen population size has been reached within the host (Wilson & Worcester,  
4 1945). Accordingly, non-linear dose- or stimulus-response relationships can be  
5 explained by the requirement for a given component to be accumulated before it can  
6 produce a measurable effect (Stock, 1999).

7

8 Three basic models can be recognized in the assemblage of matter and  
9 energy that leads to the emergence of properties. They differ according to the  
10 amplification processes which build them and cohesion forces that stabilize them.  
11 Numerous examples can be taken from the field of ecology, the theme focussing  
12 mainly on the move from organisms to ecosystems. The aim is to reconcile holistic  
13 and reductionist theories, which apply to the same subjects but interpret them quite  
14 differently (Bergandi & Blandin, 1998), and show that in the field of biology  
15 emergence is simply a property of matter.

16

## 17 **II. THE BUBBLE MODEL**

18

19 The BUBBLE model (Fig. 1) describes a system whose most important properties are  
20 conditioned by its external envelope, i.e. the skin of the BUBBLE. This outer sheet is  
21 the seat of the main cohesion forces that maintain the integrity of the system. It acts  
22 as a filter, regulating all exchanges of matter and energy between the inside and  
23 outside. The external boundary delineates the system, giving it shape and unity. This  
24 is also the zone of contact with other systems. However, the BUBBLE needs other  
25 forces in order to react to environmental influences and, thus, to maintain viability.

1 Without internal expansion/reaction forces that maintain a constant turgor or act as a  
2 skeleton, the system would collapse when faced with antagonistic effects from its  
3 surroundings.

4

5 In the real world all living organisms are BUBBLEs. They are protected by a  
6 skin, a cuticle, a shell, or at least a resistant membrane that delineates them. The  
7 periphery of living organisms is the seat of sensory functions, absorption (energy  
8 included), excretion, electrical activity and, in unicellular organisms, movement.  
9 Death of the organism may result if the integrity of this envelope is lost, either directly  
10 by leakage of internal components or indirectly through infection or toxicity. The  
11 envelope itself, which acts as an external skeleton (cuticle, shell), largely determines  
12 the shape of the organism. When the envelope is soft (skin, epidermis) it is reinforced  
13 by an internal skeleton, which can be either solid or liquid (Quillin, 1998). Near-  
14 perfect BUBBLEs, strongly protected against environmental hazards, exist as resting  
15 stages of organisms, such as eggs, cysts, spores, seeds, and also soil micro-  
16 aggregates (Kilbertus, 1980).

17

18 BUBBLEs also exist at a supra-organismal level. Territories and nests fall  
19 within this category. Physical barriers are created around them or around their  
20 offspring by nesting organisms such as ants, termites, bees, and many vertebrates.  
21 Interactions between fungi are associated with the intense production of pigments  
22 which act as signals, creating barriers which incompatible fungal partners cannot  
23 cross (Boddy, 2000). Similarly, territorial animals create barriers using sound, optical,  
24 chemical, tactile or electrical signals (McGregor, 1993). All these barriers (physical or  
25 not) act as filters and their integrity is essential for the stability and persistence of the

1 group or individual which they protect from antagonistic actions and environmental  
2 stress.

3

4       When not delineated abruptly by the environment itself (shore, cliff) the  
5 contour of ecosystems represents a biological boundary, with special features,  
6 termed the ecotone (Van der Maarel, 1990). Forest margins act as filters against  
7 alien species (Honnay, Verheyen & Hermy, 2002), pollutants (Weathers, Cadenasso  
8 & Pickett, 2001) or climatic hazards (Chen, Franklin & Spies, 1993) and exhibit a  
9 higher variety of plant and animal species (Harris, 1988). If a forest ecosystem is  
10 considered in its three-dimensional entirety, canopy included (Fig. 2), then features of  
11 the BUBBLE model appear more clearly. The photosynthetically active layer is the  
12 seat of most exchanges of matter and energy with the atmosphere. It consists of the  
13 touching crowns of all canopy and edge trees. These interconnected crowns form a  
14 skin, the properties of which, for example albedo, can be studied independently of  
15 component trees (Kawata, Ueno & Ohtani, 1995). The theory that the forest  
16 ecosystem has a skin was put forward by Oldeman (1986), but similar examples can  
17 be found also in cross sections of non-forest plant communities drawn by Watt  
18 (1947). Tree trunks, besides being pathways for exchanges between the soil and the  
19 photosynthetically active layer, are the skeleton, expanding the system upwards and  
20 giving it rigidity. After destructive events such as storms, disease outbreaks, fires or  
21 felling operations, any injury to the expanded external sheet must be repaired rapidly  
22 by regrowth or regeneration to avoid invasion by another, competing ecosystem  
23 (Ponge *et al.*, 1998).

24

1 BUBBLEs share common properties with Holons. The Holon is the basic  
2 concept of the hierarchical (holistic) paradigm, which interprets the universe as a  
3 nested assemblage of organisational levels, each level being controlled by one of  
4 higher order (Koestler, 1969). Like Holons, BUBBLEs are delineated by a 'filter' and  
5 exhibit a 'high internal connectance'. Contrary to Holons, BUBBLEs are not of a  
6 symbolic nature, they belong to the real world. They result from (i) strong connection  
7 between individual components of the skin, (ii) coexistence of compatible internal  
8 components, (iii) action/reaction forces between the two phases (inside and outside)  
9 which have been delineated by the skin. Non-exclusive interaction between  
10 components (cells, organs, organisms) is the driving force which helps to explain  
11 their appearance, development, and stability in space and time. The BUBBLE model  
12 is a structural model of an integrated system, not a superorganism in the  
13 Clementsian meaning of the ecosystem (Clements, 1916). BUBBLEs cannot be  
14 understood without a knowledge of the mechanisms that create and stabilize their  
15 external envelope and their internal skeleton when it exists. As an example, consider  
16 soap bubbles, the reference model. The coherence of the soap film which delineates  
17 the bubble is ensured by links between soap and water atoms which are regularly  
18 dispersed in a thin layer (Isenberg, 1978). The bubble itself (the soap film plus the  
19 gaseous sphere which it surrounds) is in a stable state when the cohesion forces of  
20 the film (the skin) equilibrate with the pressure of the air inside (the internal skeleton,  
21 here gaseous). This equilibrium explains the spherical shape of the bubble. However,  
22 the self-assemblage of atoms in a spheric soap film (the reductionist view) does not  
23 explain how the bubble was created. The air current which creates them (allowing a  
24 tube to be formed before the sphere closes by its own means) is a disturbance event  
25 (the holistic view) which acts at a much larger scale than that of the atom. Important

1 parameters of the bubble (size, thickness of the soap layer, composition of the  
2 internal atmosphere) cannot be understood without resorting to the event which  
3 creates it, acting at the scale of the whole. The cohesion of soap/water atoms and  
4 their self-arrangement in a thin crystalline layer explains how an air current, not  
5 acting at the scale of the atom itself, may force atoms of the soap film to surround a  
6 volume of air. Once created, the bubble may move (for instance upwards if heated)  
7 according to forces that act on its entirety (skin and skeleton).

8

9         At the ecosystem scale, BUBBLEs can be considered as the seat of  
10 coevolution. The fact that many organisms live together in a closed structure  
11 increases the number of stable interactions leading to coevolution (McMahon *et al.*,  
12 1978). In a previous paper, I argued that in the course of Earth's history, there was  
13 only a limited number of strategies by which plants, microbes and animals could  
14 associate to form terrestrial ecosystems (Ponge, 2003).

15

16         What happens when several BUBBLEs come into contact? I showed the  
17 importance of the skin for ensuring the integrity of the system. If BUBBLEs that come  
18 into contact belong to compatible types, the result will be fusion, by disappearance of  
19 the frontier separating them. Fusions between cells or cell organelles are well known.  
20 At the organism level, fusions occur more rarely, due to lack of compatibility, except  
21 in the plant kingdom as in grafting (Bormann, 1962). Fusions between compatible  
22 ecosystems occur frequently through coalescence of vegetation clumps (Connor,  
23 1986). The reverse phenomenon, fragmentation, has often been observed and  
24 theorized, under man-induced or natural influences (Collinge, 1996). Fragmentation  
25 and fusion are, in fact, two opposite aspects of the same phenomenon, when



1 BUBBLEs react to unfavourable or favourable effects of their environment. When two  
2 communities are incompatible from an ecological point of view, the passage from one  
3 to another can be described as a two-phase, fractal assemblage of non-miscible  
4 systems, involving the interplay between vegetation and soil organisms as the  
5 underlying mechanism (Ponge *et al.*, 1998). Examples of some more in-depth studies  
6 include savanna/forest and heath/forest boundaries (Bernier & Ponge, 1994; Eldridge  
7 *et al.*, 2001).

8

### 9 III. THE WAVE MODEL

10

11 The WAVE model (Fig. 3) describes patterns resulting from cyclic (periodic)  
12 processes the propagation of which is ensured in space by a chain reaction, which  
13 has been explained and modelled as 'percolation' (Broadbent & Hammersley, 1957)  
14 or 'reaction-diffusion' (Turing, 1952). Spatial patterns of units regularly dispersed as  
15 bands or patches and permanently changing into one another are the visible  
16 outcome of cyclic processes (Wissel, 1991). The model includes the cyclic process,  
17 the total surface or volume involved, and all the factors in play in the spatial  
18 assemblage of patches. Contrary to BUBBLEs, WAVEs are not delineated by a  
19 boundary. Rather, it can be said that the absence of an external envelope allows  
20 them to propagate themselves in time and space.

21

22 Before giving ecological examples, imagine a flow of cars in a traffic jam. In  
23 your own car, your main concern is with the delay while you start your car when the  
24 car in front of you starts to move. The delay is due to the need for safety, but also  
25 includes the time required by a cycle involving your sense organs, your muscles and

1 the inertia of your car. The process repeats itself at the next stop of the car in front.  
2 Now imagine you are in a helicopter above the traffic jam. What you see is a wave of  
3 alternately moving and stopping vehicles, that appears along the congested part of  
4 the road. This is the emergent property, the cycle of changes occurring from one car  
5 to another being the underlying process. The wave is the result of this cyclic process,  
6 the chain reaction being due to interactions (with inertia) between adjacent cars. In  
7 the absence of such interactions, no wave would appear, this is why it happens only  
8 during congestion or at least during dense traffic.

9

10 How can WAVEs occur among organisms and communities? First, it must be  
11 remembered that every periodic phenomenon can give rise to a WAVE, provided that  
12 (i) a chain reaction exists between repeated sequences, as during the propagation of  
13 a nerve impulse, (ii) no boundary arrests the process before it can start. A file of ants  
14 following each other's chemical signals fits the WAVE model in the same way as the  
15 above mentioned file of cars (Millonas, 1992). More generally, the propagation of a  
16 signal of any kind throughout an animal group is a WAVE.

17

18 Concentric circles occurring during the development of a colonial organism,  
19 such as fairy rings of fungi, belong to the WAVE type, too. After the start of colonial  
20 development, resources become depleted at the centre of the fungal colony (the  
21 nucleus), while the growing apices of fungal hyphae explore a new area, further from  
22 the nucleus (Gourbière, 1983). During this time, resources (litter for instance) may  
23 accumulate again at the now abandoned centre of the colony, enabling a new  
24 colonial development. Several fairy rings may thus result aligned as concentric  
25 circles. Flexible connection between successive circles occurs through alternation of

1 periods/places of depletion and accumulation of resources (Fisher, 1977). Such  
2 concentric rings, when created by fungal pathogens such as *Armillaria mellea*, may  
3 spread over kilometres and have been found to be responsible for the sequenced  
4 collapse and wave regeneration of wide areas of forests and orchards (Brown, 2002).  
5 The alternating depletion and accumulation of a resource consumed by two partners  
6 has been proposed as a non-stochastic explanation for the coexistence of species in  
7 the presence of active competition for space or nutrients (J.F. Ponge cited in Vannier,  
8 1985).

9  
10 At the ecosystem level, WAVES are better depicted as banded landscapes,  
11 such as those described in tiger bush and wave regeneration of forests. Tiger bush is  
12 a banded landscape commonly observed in African savannas on gentle slopes with  
13 periodical flooding (d'Herbès *et al.*, 2001). Underlying processes are successional,  
14 involving plants, microbes, animals, mineral and organic matter, with a weak but  
15 constant upslope displacement of the regeneration niche of a few dominant species  
16 (Eldridge *et al.*, 2001). The direction of the displacement and the interval between  
17 successive bands are dictated by the direction and angle of the slope, respectively  
18 (Tongway & Ludwig, 2001). An analogous process is involved in the wave  
19 regeneration of mountain coniferous forests, slope and wind being the driving forces  
20 of the downslope advance of even-aged lines of trees (Sprugel & Bormann, 1981). In  
21 both cases, the anisotropy of the landscape and associated factors (flooding, wind)  
22 originate and control the banded pattern (Thiéry, d'Herbès & Valentin, 1995). Each  
23 band is coherent, due to interconnection between organisms belonging to the same  
24 ecological unit or 'eco-unit' (Oldeman, 1990). Each 'eco-unit' is defined by the 'zero-  
25 event' which created it and in time by the lapse from pioneer to senescent stages of

1 the succession. Underlying processes creating 'eco-units' are both autogenic (the life  
2 history of species and the successional development of the community) and allogenic  
3 (storms, infectious diseases). When examining banded patterns at a low level of  
4 resolution, they appear as concentric circles, centered on a nucleus from which the  
5 process started (Tongway & Ludwig, 2001).

6

7 More generally, in the absence of environmental anisotropy, cyclic processes  
8 in the plant community create non-banded spatial patterns which belong to the  
9 WAVE type, too (Watt, 1947; Oldeman, 1990). They involve cyclic changes in  
10 environmental conditions, caused by the development and activity of dominant  
11 organisms and their plant, microbial and animal associates (Ponge *et al.*, 1998),  
12 which result in a mosaic assemblage of developmental stages of one ecosystem  
13 (Watt, 1947; Oldeman, 1990).

14

15 All these phenomena exhibit emergent properties which can be observed,  
16 measured and predicted independently of the unit sequences which compose them  
17 (holistic concept). However, these properties cannot be adequately understood and  
18 described mathematically without a knowledge of the mechanisms at play within unit  
19 sequences (reductionist concept). An abundance of theoretical literature exists on  
20 dynamic spatial patterns involving a flexible connection between individual  
21 sequences (Bonabeau, 1997).

22

#### 23 **IV. THE CRYSTAL MODEL**

24

1 Contrary to WAVES, where connection between units is flexible, a rigid connection  
2 between unit components is the main characteristic of CRYSTALS (Fig. 4). Here, too,  
3 repetitiveness builds up the system, and explains its emergent properties. Positive  
4 feedback or synergistic reaction (Ashby, 1956) is at play in the rapid passage from  
5 chaos to order which is typical of CRYSTAL development, starting from a nucleus  
6 which acts as a template for the organization of the whole. As a corollary, any part of  
7 a CRYSTAL exhibits the same properties as the whole CRYSTAL. When several  
8 CRYSTALS come into contact, they may undergo attraction/repulsion forces, causing  
9 fusion or constant spacing, thereby constructing higher-order CRYSTALS, as in clay  
10 (Olson, Thompson & Wilson, 2000) and cellulose lattices (Dey & Harborne, 1997).  
11 CRYSTALS exhibit high stability against external influences, but they may  
12 disintegrate and return to chaos when a local disruption of the assemblage spreads  
13 to the whole CRYSTAL by a chain reaction, e.g. during the dissolution of a salt  
14 crystal (Lasaga & Lüttge, 2003).

15

16 At the organismal level CRYSTALS are commonly observed in tight  
17 assemblages of identical unit components, for instance in membranes (Singer &  
18 Nicolson, 1972), cell walls (Dey & Harborne, 1997) and parenchyma (Andersen *et al.*,  
19 1997). Properties of CRYSTALS are also exhibited by arborescences, which repeat  
20 indefinitely in a fractal manner, containing the same pattern of branching, as in coral  
21 reefs, tree crowns, and root systems. The pattern is dictated by the genetically coded  
22 architectural model (Hallé, Oldeman & Tomlinson, 1978), interactions between unit  
23 components (as long as they come into contact), and interactions with the immediate  
24 environment (Sachs & Novoplansky, 1995). The 'constructal' theory explains how  
25 multiple interactions between unit components may form complex, stable

1 assemblages with optimal use of matter and energy (Bejan, 2000). This justifies the  
2 inclusion of fractal structures in the CRYSTAL model.

3

4 Strongly interacting organisms in a CRYSTAL may, by oscillatory processes  
5 (trial-and-error behaviour included), optimize their shape and position within a group  
6 at a supra-organismal level. Examples can be found in the arrangement of tree  
7 crowns in forest canopies and of individuals in bird flocks (James, Bennett & Krause,  
8 2004). Oscillations of individual trees within a forest canopy change the shape of the  
9 tree crown and are at the origin of a space between adjoining crowns, called 'crown  
10 shyness' (Rudnicki, Lieffers & Sillins, 2003). Similarly, dense animal aggregations  
11 optimize benefit/cost ratios for foraging and escape of predators (James *et al.*, 2004).  
12 Individual replacements may occur without endangering the group, just as atoms  
13 may jump in true crystals without endangering the whole structure (Huntington,  
14 1975). Likewise, behavioural interactions within a social group can be interpreted as  
15 CRYSTALS (Granovetter, 1978), as can termites and bees nests (Courtois &  
16 Heymans, 1991).

17

## 18 **V. BIOLOGICAL ASSEMBLAGES OF BUBBLES, WAVES AND CRYSTALS**

19

20 The main properties of BUBBLES, WAVES and CRYSTALS are summarized in Table  
21 1, and some biological and ecological examples are shown in Table 2.

22

23 The outer envelope of BUBBLES is responsible for their high resistance, i.e.  
24 their direct reaction to external, antagonistic forces (Holling, 1973), and it is the seat  
25 of connection forces (Fig. 1). BUBBLES as ecological systems include a number of

1 biological components which can evolve together in a common, stable space.  
2 Organisms living in BUBBLEs develop numerous competitive and mutualistic  
3 interactions (Oldeman, 1990; Ponge, 2003). At the ecosystem level the appearance  
4 of the skin of BUBBLEs is explained by (i) between-individual interference, which  
5 forces the organisms to grow organs used for long-distance dispersal and energy  
6 acquisition away from the substratum, (ii) more interaction at the periphery with  
7 external factors such as light and wind (water currents for aquatic ecosystems).  
8 Surprisingly, such patterns have been modelled and explained at the molecular  
9 scale, as in soap bubbles (Isenberg, 1978), but not at the scale of organisms, social  
10 groups and ecosystems, despite their common occurrence. An exception is the work  
11 of Oldeman (1986, 1990) and Rossignol *et al.* (1998), which explained how complex  
12 ecosystem architecture is governed by simple rules of coexistence and how distinct  
13 structures appear at the boundary of ecosystems.

14

15 As with other periodic phenomena, WAVEs are characterized by the absence  
16 of defined limits in space and time. They are in a dynamic state of equilibrium which  
17 confers upon them low resistance but high 'resilience' to external pressure.  
18 'Resilience' is an autogenic process in which the system is reconstructed after an  
19 external pressure has destroyed all or part of it (Holling, 1973). WAVEs require some  
20 degree of homogeneity in the environment to develop as regular lines or patches,  
21 according to anisotropy or isotropy of the environment (Thiéry *et al.*, 1995). In turn,  
22 they create a reversible (flexible) heterogeneity as a consequence of their  
23 development (Watt, 1947; Oldeman, 1990).

24

1           Contrary to the two previous cases, CRYSTALS exhibit an homogeneous  
2 structure. Events that create them can be accidental (a nucleus, followed by the the  
3 self-reinforcing assemblage of dispersed components), as in bird flocks (James *et al.*,  
4 2004), or they may result from strong interactions between adjoining components, as  
5 in forest canopies (Rudnicki *et al.*, 2003). Like BUBBLES, CRYSTALS are structured,  
6 not dynamic models. At first, CRYSTALS may appear to exhibit many features in  
7 common with BUBBLES, and can be confused with them. Both are stable against  
8 external influences and both are weakly dynamic. The differences lie in the origin of  
9 the strong continuity, which is in the external envelope of BUBBLES and in the whole  
10 matrix of CRYSTALS. The BUBBLE model allows disorder to occur on the inside  
11 without endangering the whole structure, unlike CRYSTALS where local disorder may  
12 cause the whole system to collapse.

13

14           What relationships exist between BUBBLES, WAVES and CRYSTALS? In the  
15 biological world, they are currently found nested. The skin of a BUBBLE belongs to  
16 the CRYSTAL model, which confers on it a high structural stability. Examples can be  
17 found in cell walls (Dey & Harborne, 1997), epidermis (Esau, 1965), and forest  
18 canopies (Oldeman, 1986). WAVES can also be perceived in the outer envelope of  
19 BUBBLES, provided a vibration is propagated. This can be seen at the surface of  
20 ciliate cells (Naitoh, 1966), and electrical- or molecular-mediated waves are known at  
21 the surface of organs and organisms (Kondo & Asai, 1995; Aliev, Richards &  
22 Wikswo, 2000). The propagation in space of the mechanical effect of wind on forest  
23 canopies also follows the same principle (Lee, 1997). Individual bands in banded  
24 landscapes, and individual patches in ecosystem mosaics ('eco-units' *sensu*  
25 Oldeman, 1990), exhibit a structure which belongs to the BUBBLE model (Watt,



1 1947; Oldeman, 1990; Tongway & Ludwig, 2001). The 'zero-event', *sensu* Oldeman  
2 (1990), is analogous to the air flush which initiates the development of soap bubbles.  
3 More generally, assemblages (cells, organs, organisms) included within BUBBLES,  
4 WAVES and CRYSTALS follow in turn the BUBBLE, WAVE or CRYSTAL model,  
5 according to the scale and the conditions that allow their start and development.

6

7 Each time a BUBBLE, WAVE or CRYSTAL appears, a 3-D discontinuity is  
8 created (organ, organism, ecosystem and landscape boundaries), explaining the  
9 fractal discontinuities that can be observed when zooming over a range of scales  
10 (Gonzato, Mulargia & Ciccotti, 2000).

11

## 12 **VI. MODELLING EMERGENCE, A NEW CHALLENGE FOR ECOLOGY**

13

14 All patterns and processes depicted by BUBBLES, WAVES and CRYSTALS, and their  
15 multi-scale combinations, may help to describe and explain most emergent  
16 properties of organisms and ecological systems. Modelling complexity, more  
17 especially in the field of ecology and biological development, has been a challenge  
18 for nearly a century, if we exclude the geometric representation of human proportions  
19 by Leonardo da Vinci, largely tainted with hermetism. As early as 1917, d'Arcy  
20 Thompson showed that a limited set of equations could be used to derive the shape  
21 of a wide variety of organisms (he used fish as an example) by distorting a unique  
22 geometric model. Subsequently, developments in computer science helped to mimic  
23 properties of natural systems (Holland, 1975). The advent of cybernetics (Wiener,  
24 1948) allowed complex physiological, social and ecological processes of control and  
25 regulation to be described and better understood (Laborit, 1968; Negrotti, 1983;

1 Bergandi, 2000). As a consequence, there appeared to be a cleavage between  
2 people that observed and classified the living world ('naturalists') and those that  
3 recreated it on their computers ('theoreticians'). The second half of the 20<sup>th</sup> century  
4 was marked by a clear departure between 'upper' and 'lower' scientists, despite  
5 repeated claims that models should incorporate a better knowledge of underlying  
6 processes without which models would be a waste of time (de Wit, 1986). The need  
7 to study the real world with its chances, individualities and 'fuzzy' contours, rather  
8 than theoretically sound but unrealistic models tending to perfection, has been  
9 stressed by field-experienced authors, who derived ecosystem-level properties from  
10 a good knowledge of biological traits of dominant organisms and their interactions  
11 (Watt, 1947; Oldeman, 1990; Coffin & Urban, 1993; Grime, 1998). However,  
12 theoretical models aimed at predicting properties at ecosystem level (Loreau, 1998;  
13 Ponsard, Arditi & Jost, 2000) still do not take into account chances and  
14 individualities, as depicted by field conditions and past history of sites. Following the  
15 interest of physicists in biological science and the acceptance of the unpredictable by  
16 theoreticians, accidental events that may cause departure from a deterministic trend  
17 are now incorporated in predictive ecological models (Stone & Ezrati, 1996;  
18 Bonabeau, 1997). Recent, promising approaches include attempts to incorporate  
19 basic biological processes and accidental events into ecosystem modelling (Favier *et*  
20 *al.*, 2004).

21  
22 Landscape ecology (Urban, O'Neill & Shugart, 1987), aimed at identifying  
23 emergent properties without an *a priori* hypothesis, failed to reveal true, integrated  
24 systems because of its own operational concepts, favouring patterns over processes  
25 and holism over reductionism (Bergandi & Blandin, 1998). When tautologically based

1 on sophisticated methods or theories, science may drive us up blind alleys  
2 (Oldeman, 1990). Instead, in a more modest manner, we should in a first explanatory  
3 step let patterns emerge from our observation of the real world (Benzécri, 1969),  
4 discern emergent properties, and only then investigate underlying processes by  
5 experimental and theoretical methods. Today, this is not the mainstream of scientific  
6 practice, which creates theory as a first, decisive step. However, it could well move  
7 into prominence in the near future, if and when interest in more realistic approaches  
8 increases.

9

## 10 **VII. CONCLUSIONS**

11

- 12 1. The Emergence of properties can be understood from a materialistic point of  
13 view, by taking into account principles that govern the build-up, maintenance  
14 and mutual relationships of biological and ecological assemblages
- 15 2. Three self-assembled models can be recognized that explain how properties  
16 may emerge at organism and community levels: BUBBLEs, WAVEs and  
17 CRYSTALs
- 18 3. These models differ in cohesion forces and dynamic properties
- 19 4. These elemental models combine, in a nested way, to form complex biological  
20 and ecological systems

21

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23

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4

## 5 **VIII. REFERENCES**

6

7 Aliev, R.R., Richards, W. & Wikswo, J.P. (2000). A simple nonlinear model of  
8 electrical activity in the intestine. *Journal of Theoretical Biology* **204**, 21-28.

9 Andersen, M.E., Eklund, C.R., Mills, J.J., Barton, H.A. & Birnbaum, L.S. (1997). A  
10 multicompartiment geometric model of the liver in relation to regional induction  
11 of cytochrome P450s. *Toxicology and Applied Pharmacology* **144**, 135-144.

12 Ashby, W.R. (1956). *An Introduction to Cybernetics*. London: Chapman and Hall.

13 Bejan, A. (2000). *Shape and Structure, from Engineering to Nature*. Cambridge:  
14 Cambridge University Press.

15 Benzécri, J.P. (1969). Statistical analysis as a tool to make patterns emerge from  
16 data. In *Methodologies of Pattern Recognition* (ed. S Watanabe), pp. 35-74.  
17 New York: Academic Press.

18 Bergandi, D. (2000). Eco-cybernetics: the ecology and cybernetics of missing  
19 emergences. *Kybernetes* **29**, 928-942.

20 Bergandi, D. & Blandin, P. (1998). Holism vs. reductionism: do ecosystem ecology  
21 and landscape ecology clarify the debate? *Acta Biotheoretica* **46**, 185-206.

22 Bernier, N. & Ponge, J.F. (1994). Humus form dynamics during the sylvogenetic  
23 cycle in a mountain spruce forest ecosystem. *Soil Biology and Biochemistry*  
24 **26**, 183-220.

- 1 Boddy, L. (2000). Interspecific combative interactions between wood-decaying  
2 basidiomycetes. *FEMS Microbiology Letters* **31**, 185-194.
- 3 Bonabeau, E. (1997). Flexibility at the edge of chaos: a clear example from foraging  
4 in ants. *Acta Biotheoretica* **45**, 29-50.
- 5 Bormann, F.H. (1962). Root grafting and non-competitive relationships between  
6 trees. In *Tree growth* (ed. Kozlowski, T.T.), pp. 237-246. New York: Ronald  
7 Press.
- 8 Broadbent, S. & Hammersley, J. (1957). Percolation processes. I. Crystals and  
9 mazes. *Proceedings of the Cambridge Philosophical Society* **53**, 629-641.
- 10 Brown, A.K. (2002). Historical oak woodland detected through *Armillaria mellea*  
11 damage in fruit orchards. *USDA Forest Service General Technical Report*  
12 *PSW-GTR-184*.
- 13 Chen, J., Franklin, J.F. & Spies, T.A. (1993). Contrasting microclimates among  
14 clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and*  
15 *Forest Meteorology* **63**, 219-237.
- 16 Clements, F.E. (1916). *Plant Succession: an Analysis of the Development of*  
17 *Vegetation*. Washington: Carnegie Institution of Washington.
- 18 Coffin, D.P. & Urban, D.L. (1993). Implications of natural history traits to system-level  
19 dynamics: comparisons of a grassland and a forest. *Ecological Modelling* **67**,  
20 147-178.
- 21 Collinge, S.K. (1996). Ecological consequences of habitat fragmentation: implications  
22 for landscape architecture and planning. *Landscape and Urban Planning* **36**,  
23 59-77.
- 24 Connor, E.F. (1986). The role of Pleistocene forest refugia in the evolution and  
25 biogeography of tropical biotas. *Trends in Ecology and Evolution* **1**, 165-168.

- 1 Courtois, P.J. & Heymans, F. (1991). A simulation of the construction process of a  
2 termite nest. *Journal of Theoretical Biology* **153**, 469-475.
- 3 d'Arcy Thompson, W. (1917). *On Growth and Form*. Cambridge: Cambridge  
4 University Press.
- 5 de Wit, C.T. (1986). Modelling agricultural production. *Acta Horticulturae* **184**, 59-70.
- 6 d'Herbès, J.M., Valentin, C., Tongway, D.J. & Leprun, J.C. (2001). Banded  
7 vegetation patterns and related structures. In *Banded Vegetation Patterning in*  
8 *Arid and Semiarid Environnements* (eds. Menaut, J.C. & Walker, B.), pp. 1-19.  
9 New York: Springer.
- 10 Dey, P.M. & Harborne, J.B. (1997). *Plant Biochemistry*. San Diego: Academic Press.
- 11 Eldridge, D.J., Lepage, M., Bryannah, M.A. & Ouedraogo, P. (2001). Soil biota in  
12 banded landscapes. In *Banded Vegetation Patterning in Arid and Semiarid*  
13 *Environnements* (eds. Menaut, J.C. & Walker, B.), pp. 105-131. New York:  
14 Springer.
- 15 Esau, K. (1965). *Plant Anatomy*. New York: John Wiley.
- 16 Favier, C., Chave, J., Fabing, A., Schwartz, D. & Dubois, M.A. (2004). Modelling  
17 forest-savanna mosaic dynamics in man-influenced environments: effects of  
18 fire, climate and soil heterogeneity. *Ecological Modelling* **171**, 85-102.
- 19 Fisher, R.F. (1977). Nitrogen and phosphorus mobilization by the fairy ring fungus,  
20 *Marasmius oreades* (Bolt.) Fr. *Soil Biology and Biochemistry* **9**, 239-241.
- 21 Gonzato, G., Mulargia, F. & Ciccotti, M. (2000). Measuring the fractal dimensions of  
22 ideal and actual objects: implications for application in geology and  
23 geophysics. *Geophysical Journal International* **142**, 108-116.

- 1 Gourbière, F. (1983). Pourriture blanche de la litière d'*Abies alba* Mill. II. Répartition  
2 spatio-temporelle et activité annuelle des Basidiomycètes du genre *Collybia*.  
3 *Revue d'Écologie et de Biologie du Sol* **20**, 461-474.
- 4 Granovetter, M. (1978). Threshold models of collective behavior. *American Journal of*  
5 *Sociology* **83**, 1420-1443.
- 6 Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and  
7 founder effects. *Journal of Ecology* **86**, 902-910.
- 8 Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978). *Tropical Trees and Forests: an*  
9 *Architectural Analysis*. Springer, Berlin.
- 10 Harris, L.D. (1988). Edge effects and conservation of biotic diversity. *Conservation*  
11 *Biology* **2**, 330-332.
- 12 Henle, P. (1942). The status of emergence. *The Journal of Philosophy* **39**, 486-493.
- 13 Holland, J.H. (1975). *Adaptation in Natural and Artificial Systems. An Introductory*  
14 *Analysis with Applications to Biology, Control, and Artificial Intelligence*. Ann  
15 Arbor: The University of Michigan Press.
- 16 Holland, J.H. (1998). *Emergence: from Chaos to Order*. Oxford: Oxford University  
17 Press.
- 18 Holling, C.S. (1973). Resilience and stability of ecological systems. *Annual Review of*  
19 *Ecology and Systematics* **4**, 1-23.
- 20 Honnay, O., Verheyen, K. & Hermy, M. (2002). Permeability of ancient forest edges  
21 for weedy plant species invasion. *Forest Ecology and Management* **161**, 109-  
22 122.
- 23 Huntington, H.B. (1975). Effect of driving forces on atom motion. *Thin Solid Films* **25**,  
24 265-280.

- 1 Isenberg, C. (1978). *The Science of Soap Film and Soap Bubbles*. Somerset:  
2 Woodspring Press.
- 3 James, R., Bennett, P.G. & Krause, J. (2004). Geometry for mutualistic and selfish  
4 herds: the limited domain of danger. *Journal of Theoretical Biology* **228**, 107-  
5 113.
- 6 Kawata, Y., Ueno, S. & Ohtani, A. (1995). The surface albedo retrieval of  
7 mountainous forest area from satellite MSS data. *Applied Mathematics and*  
8 *Computation* **69**, 41-59.
- 9 Kilbertus, G. (1980). Étude des microhabitats contenus dans les agrégats du sol.  
10 Leur relation avec la biomasse bactérienne et la taille des procaryotes  
11 présents. *Revue d'Écologie et de Biologie du Sol* **17**, 543–557.
- 12 Koestler, A. (1969). Beyond atomism and holism. The concept of holon. In *Beyond*  
13 *Reductionism. New Perspectives in the Life Sciences* (eds. Koestler, A. &  
14 Smythies, J.R.), pp. 192-232. London: Hutchinson.
- 15 Kondo, S. & Asai, R. (1995). A reaction-diffusion wave on the skin of the marine  
16 angelfish *Pomacanthus*. *Nature* **376**, 765-768.
- 17 Laborit, H. (1968) *Biologie et Structure*. Paris: Gallimard.
- 18 Lasaga, A.C. & Lüttge, A. (2003). A model for crystal dissolution. *European Journal*  
19 *of Mineralogy* **15**, 603-615.
- 20 Lee, X. (1997). Gravity waves in a forest: a linear analysis. *Journal of the*  
21 *Atmospheric Sciences* **54**, 2574-2585.
- 22 Levin, S.A. (2000). Multiple scales and the maintenance of biodiversity. *Ecosystems*  
23 **3**, 498-506.



- 1 Loreau, M. (1998). Biodiversity and ecosystem functioning: a mechanistic model.  
2 *Proceedings of the National Academy of Sciences of the United States of*  
3 *America* **95**, 5632-5636.
- 4 McGregor, P.K. (1993). Signalling in territorial systems: a context for individual  
5 identification, ranging and eavesdropping. *Philosophical Transactions of the*  
6 *Royal Society of London, series B, Biological Sciences* **340**, 237-244.
- 7 McMahon, J.A., Phillips, D.L., Robinson, J.V. & Schimpf, D.J. (1978). Levels of  
8 biological organization: an organism-centered approach. *BioScience* **28**, 700-  
9 704.
- 10 Mayr, E. (1982). *The Growth of Biological Thought*. Cambridge: Belknap.
- 11 Millonas, M. (1992). A connectionist type model of self-organized foraging and  
12 emergent behavior in ant swarms. *Journal of Theoretical Biology* **159**, 529-  
13 552.
- 14 Naitoh, Y. (1966). Reversal reponse elicited in nonbeating cilia of *Paramecium* by  
15 membrane depolarization. *Science* **154**, 660-662.
- 16 Negrotti, M. (1983). *Intelligenza Artificiale e Scienze Sociali*. Milano: Angeli.
- 17 Oldeman, R.A.A. (1986). On the limits of forest ecosystems: do they have skins? In  
18 *Proceedings of the 18<sup>th</sup> IUFRO World Congress, Ljubljana, Yugoslavia, Sept.*  
19 *7-21, Division 6, General Subjects*, pp. 312-324.
- 20 Oldeman, R.A.A. (1990). *Forests: Elements of Silvology*. Berlin: Springer.
- 21 Olson, C.G., Thompson, M.L. & Wilson, M.A. (2000). Phyllosilicates. In *Handbook of*  
22 *Soil Science* (ed. Sumner, M.E.), pp. F77-F123. Boca Raton: CRC Press.
- 23 Ponge, J.F. (2003). Humus forms in terrestrial ecosystems: a framework to  
24 biodiversity. *Soil Biology and Biochemistry* **35**, 935-945.

- 1 Ponge, J.F., André, J., Zackrisson, O., Bernier, N., Nilsson, M.C. & Gallet, C. (1998).  
2 The forest regeneration puzzle: biological mechanisms in humus layer and  
3 forest vegetation dynamics. *BioScience* **48**, 523-530.
- 4 Ponsard, S., Arditi, R. & Jost, C. (2000). Assessing top-down and bottom-up control  
5 in a litter-based soil macroinvertebrate food chain. *Oikos* **89**, 524-540.
- 6 Quillin, K.J. (1998). Ontogenic scaling of hydrostatic skeletons: geometric, static  
7 stress and dynamic stress scaling of the earthworm *Lumbricus terrestris*.  
8 *Journal of Experimental Biology* **201**, 1871-1883.
- 9 Rossignol, M., Rossignol, L., Oldeman, R.A.A. & Benzine-Tizroutine, S. (1998).  
10 *Struggle of Life or the Natural History of Stress and Adaptation*. Heelsum:  
11 Treemail.
- 12 Rudnicki, M., Lieffers, V.J. & Sillins, U. (2003). Stand structure governs the crown  
13 collisions of lodgepole pine. *Canadian Journal of Forest Research* **33**, 1238-  
14 1244.
- 15 Sachs, T. & Novoplansky, A. (1995). Tree form: architectural models do not suffice.  
16 *Israel Journal of Plant Sciences* **43**, 203-212.
- 17 Singer, S.J. & Nicolson, G.L. (1972). The fluid mosaic model of the structure of  
18 membranes. *Science* **175**, 720-731.
- 19 Sprugel, D.G. & Bormann, F.H. (1981). Natural disturbance and the steady state in  
20 high-altitude balsam fir forests. *Science* **211**, 390-393.
- 21 Stock, A.M. (1999). A nonlinear stimulus-response relation in bacterial chemotaxis.  
22 *Proceedings of the National Academy of Sciences of the United States of*  
23 *America* **96**, 10945-10947.
- 24 Stone, L. & Ezrati, S. (1996). Chaos, cycles and spatiotemporal dynamics in plant  
25 ecology. *Journal of Ecology* **84**, 279-291.

- 1 Thiéry, J.M., d'Herbès, J.M. & Valentin, C. (1995). A model simulating the genesis of  
2 banded vegetation patterns in Niger. *Journal of Ecology* **83**, 497-507.
- 3 Tongway, D.J. & Ludwig, J.A. (2001). Theories on the origin, maintenance dynamics,  
4 and functioning of banded landscapes. In *Banded Vegetation Patterning in*  
5 *Arid and Semiarid Environnements* (eds. Menaut, J.C. & Walker, B.), pp. 20-  
6 31. New York: Springer.
- 7 Turing, A. (1952). The chemical basis of morphogenesis. *Philosophical Transactions*  
8 *of the Royal Soceity of London, Series B, Biological Sciences* **237**, 37-72.
- 9 Urban, D.L., O'Neill, R.V. & Shugart, H.H.Jr. (1987). Landscape ecology. A  
10 hierarchical perspective can help scientists understand spatial patterns.  
11 *BioScience* **37**, 119-127.
- 12 Van der Maarel, E. (1990). Ecotones and ecoclines are different. *Journal of*  
13 *Vegetation Science* **1**, 135-138.
- 14 Vannier, G. (1985). Modes d'exploitation et de partage des ressources alimentaires  
15 dans le système saprophage par les microarthropodes du sol. *Bulletin*  
16 *d'Écologie* **16**, 19-34.
- 17 Watt, A.S. (1947). Pattern and process in the plant community. *Journal of Ecology*  
18 **35**, 1-22.
- 19 Weathers, K.C., Cadenasso, M.L. & Pickett, S.T.A. (2001). Forest edges as nutrient  
20 and pollutant concentrators: potential synergisms between fragmentation,  
21 forest canopies, and the atmosphere. *Conservation Biology* **15**, 1506-1514.
- 22 Wiener, N. (1948). *Cybernetics*. Cambridge, Massachusetts: Riverside Press.
- 23 Wilson, E.B. & Worcester, J. (1945). The law of mass action in epidemiology.  
24 *Proceedings of the National Academy of Sciences of the United States of*  
25 *America* **31**, 24-34.

- 1 Wissel, C. (1991). A model for the mosaic-cycle concept. In *The Mosaic-Cycle*
- 2 *Concept of Ecosystems* (ed. Remmert, H.), pp. 22-45. Berlin: Springer.

**Table 1.** Main properties of the three models describing systems with emergent properties

|                               | BUBBLE     | WAVE     | CRYSTAL |
|-------------------------------|------------|----------|---------|
| Outer envelope                | Yes        | No       | No      |
| Stability (resistance)        | High       | Low      | High    |
| Stability (resilience)        | Medium     | High     | Low     |
| Connection                    | Pellicular | Flexible | Massive |
| Internal variation (disorder) | High       | Medium   | Low     |
| Autogenic build-up            | Yes        | No       | Yes     |
| Allogenic build-up            | Yes        | Yes      | No      |

**Table 2.** Some examples of BUBBLES, WAVES and CRYSTALS cited in the text

|                 | <b>Examples</b>                                     | <b>References</b>   |
|-----------------|---|---|
| <b>BUBBLES</b>  | Boundaries of ecosystems as skins                   | Watt (1947); Oldeman (1986); Kawata <i>et al.</i> (1995); Harris (1988); Van der Maarel (1990); Chen <i>et al.</i> (1993); Weathers <i>et al.</i> (2001); Honnay <i>et al.</i> (2002) |
|                 | Fusion and fragmentation                            | Bormann (1962); Connor (1986); Bernier & Ponge (1994); Collinge (1996); Ponge <i>et al.</i> (1998); Eldridge <i>et al.</i> (2001)   |
|                 | Internal skeleton (liquid)                          | Quillin (1998)  |
|                 | Territories   | McGregor (1993); Boddy (2000)   |
|                 | Mutualistic interactions between components         | McMahon <i>et al.</i> (1978); Ponge (2003)  |
|                 | Soil micro-aggregates                               | Kilbertus (1980)  |
| <b>WAVES</b>    | Surface of ciliate cells                            | Naitoh (1966)   |
|                 | Surface of organs                                   | Aliev <i>et al.</i> (2000)  |
|                 | Banded morphogenesis                                | Turing (1952); Kondo & Asai (1995)  |
|                 | Surface of ecosystems                               | Lee (1997)  |
|                 | Ant files   | Millonas (1992); Bonabeau (1997)  |
|                 | Fairy rings   | Fisher (1977); Gourbière (1983); Brown (2002)   |
|                 | Competitive alternance                              | Vannier (1985)  |
|                 | Wave regeneration                                   | Sprugel & Bormann (1981)  |
|                 | Patch dynamics                                      | Watt (1947); Oldeman (1990); Wissel (1991); Ponge <i>et al.</i> (1998)  |
|                 | Banded landscapes                                   | Thiéry <i>et al.</i> (1995); d'Herbès <i>et al.</i> (2001); Tongway & Ludwig (2001); Eldridge <i>et al.</i> (2001)  |
| <b>CRYSTALS</b> | Cell walls, membranes                               | Singer & Nicolson (1972); Dey & Harborne (1997)   |
|                 | Epidermis   | Esau (1965)   |
|                 | Parenchyma  | Andersen <i>et al.</i> (1997)   |
|                 | Arborescences, fractal patterns, constructal theory | Hallé <i>et al.</i> (1978); Sachs & Novoplansky (1995); Bejan (2000); Gonzato <i>et al.</i> (2000)  |
|                 | Bird flocks   | James <i>et al.</i> (2004)  |
|                 | Forest canopies                                     | Oldeman (1986); Rudnicki <i>et al.</i> (2003)   |
|                 | Social groups                                       | Granovetter (1978)  |
|                 | Nests of social animals (bees, termites)            | Courtois & Heymans (1991)   |

1 **FIGURE LEGENDS**

2

3 **Fig. 1.** The BUBBLE system.

4

5 **Fig. 2.** The forest, described as a BUBBLE.

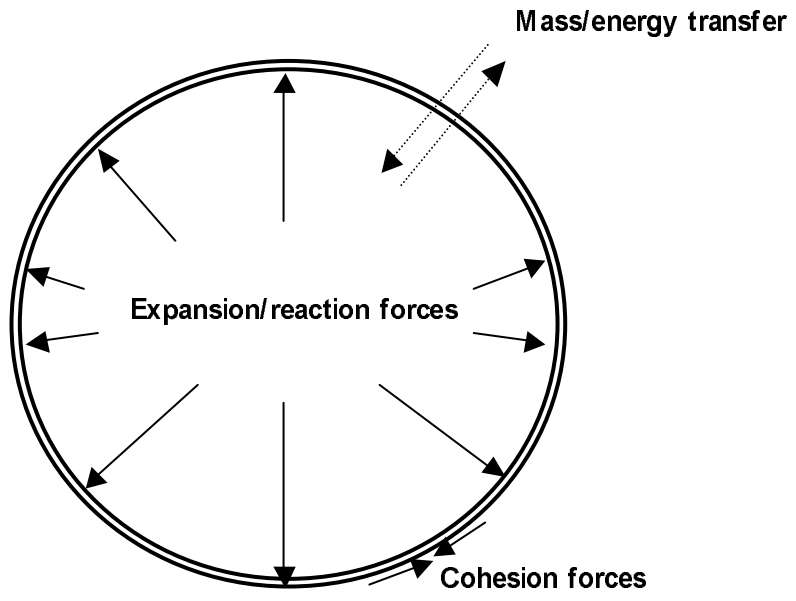
6

7 **Fig. 3.** The WAVE system.

8

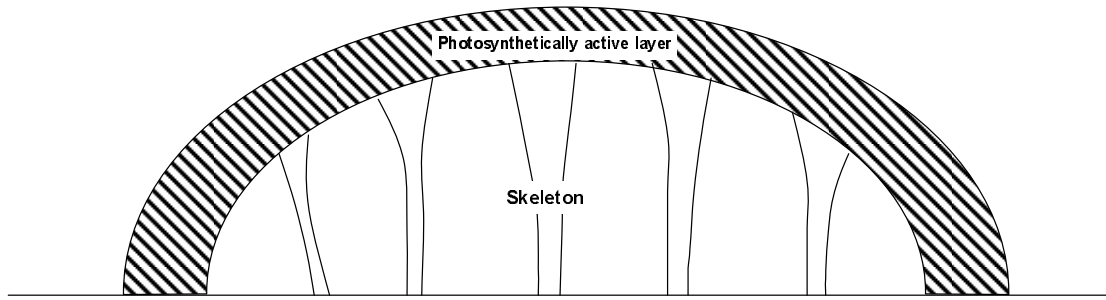
9 **Fig. 4.** The CRYSTAL system.

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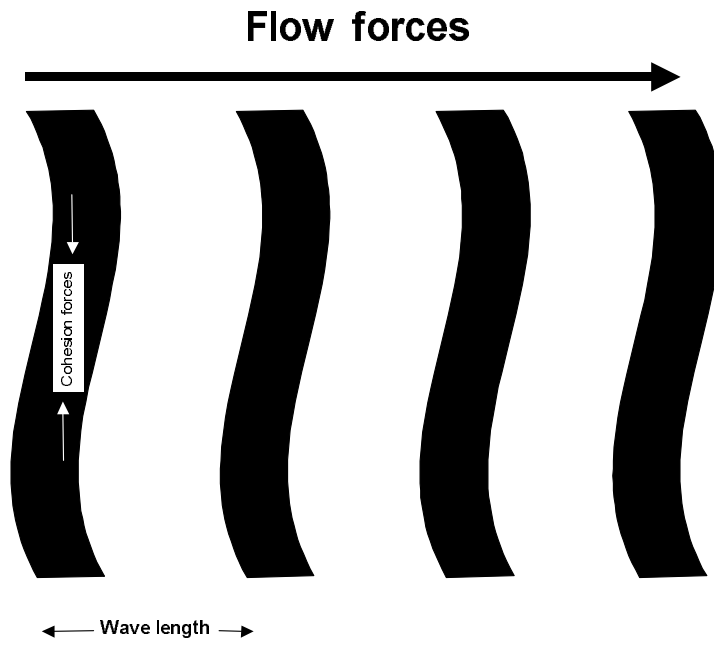
**Fig. 1**





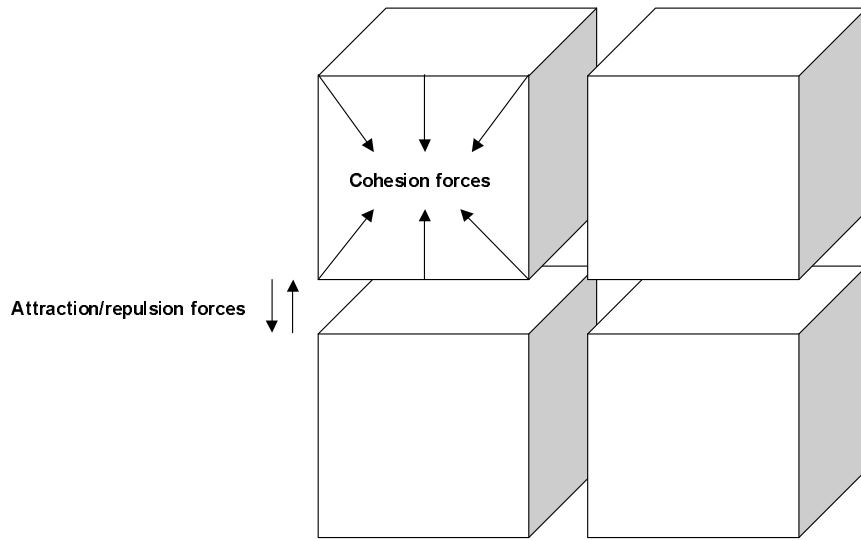
1  
2 **Fig. 2**

1



2 Fig. 3

1



2 Fig. 4