Epigenetic opportunities for Evolutionary Computation

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Abstract

Evolutionary Computation is a group of biologically inspired algorithms used to solve complex optimisation problems. It can be split into Evolutionary Algorithms, which take inspiration from genetic inheritance, and Swarm Intelligence algorithms, that take inspiration from cultural inheritance. However, recent developments have focused on computational or mathematical adaptions, leaving their biological roots behind. This has left much of the modern evolutionary literature relatively unexplored.

To understand which evolutionary mechanisms have been considered, and which have been overlooked, this paper breaks down successful bio-inspired algorithms under a contemporary biological framework based on the Extended Evolutionary Synthesis, an extension of the classical, genetics focussed, Modern Synthesis. The analysis shows that Darwinism and the Modern Synthesis have been incorporated into Evolutionary Computation but that the Extended Evolutionary Synthesis has been broadly ignored beyond cultural inheritance, incorporated in the sub-set of Swarm Intelligence algorithms, evolvability, through CMA-ES, and multilevel selection, through Multi-Level Selection Genetic Algorithm.

The framework shows a missing gap in epigenetic inheritance for Evolutionary Computation, despite being a key building block in modern interpretations of how evolution occurs. Epigenetic inheritance can explain fast adaptation, without changes in an individual’s genotype, by allowing biological organisms to self-adapt quickly to environmental cues, which, increases the speed of convergence while maintaining stability in changing environments. This leaves a diverse range of biologically inspired mechanisms as low hanging fruit that should be explored further within Evolutionary Computation.

Keywords: Evolutionary Algorithms, Evolutionary Computation, Swarm Intelligence, Evolutionary biology, Non-genetic inheritance

1. Maximising the potential from biological analogies

Evolutionary Computation has emerged as one of the most studied branches of Artificial Intelligence. Hundreds of approaches have been reported over the years, based on different bio-inspired behaviours. However, it is difficult to determine the uniqueness of each algorithm when new approaches only change the vocabulary and not the underlying mathematics. The constant addition of new algorithms has led to discussions about whether the biological analogies have gone too far with some arguing that chasing new novel metaphors for algorithms risks moving attention away from innovative ideas that make a real difference. However, new genetic algorithms, such as...
cMLSGA (co-evolutionary Multilevel Selection Genetic Algorithm) [2], have successfully explored additional non-genetic or indirectly genetic mechanisms, and found benefits that improve performance on a growing number of practical problems [3 [4]. The key to success for Evolutionary Computation appears to be exploration of new mechanisms without repeatedly exploring the same mechanisms under a new name.

In evolutionary theory, the Modern Synthesis [5] was developed throughout the first half of the 20th century to combine the ideas of Darwin and Wallace’s evolution by natural selection [6 [7], and Mendel’s principles of inheritance [8]. Despite the contribution to evolution from these mechanisms, there is growing evidence that suggests that non-genetic inheritance also has a strong effect. New research into the concepts of non-genetic inheritance suggests that the ideas of the Modern Synthesis should be extended [9 [10] to include the effects of epigenetics, cultural inheritance, parental and environmental effects, and multilevel selection. However, Evolutionary Computation focuses on a relatively small part of evolutionary theory with most Evolutionary Algorithms directly comparable to the concepts of the Modern Synthesis and Swarm Intelligence compared directly to cultural inheritance, despite the number of algorithms in Evolutionary Computation. Figure 1 shows the concepts of the Modern Synthesis and the Extended Evolutionary Synthesis, and highlights the concepts which have been explored. While the genetic concepts of Darwinism and the Modern Synthesis have been studied in detail, only a few concepts from the Extended Evolutionary Synthesis have been explored for Evolutionary Computation. There have only been limited efforts to bring these other non-genetic inheritance concepts to the field.

There are potential benefits to investigating the outstanding evolutionary concepts not routinely included in Evolutionary Algorithms, as demonstrated by CMA-ES and MLSGA. In addition to those already explored there are plenty of examples of mechanisms that have not been included such as: plasticity, which leads to faster adaptation in the natural world [11], and maternal effects, which can increase the rate of phenotypic evolution in changing environments while slowing it down in stable environments to maintain optimal phenotypes [12]. However, to help make distinctions between different novel algorithms it is important to understand the differences in their mechanisms, which can be aided through a better understanding of the underlying biological concepts and how close the new algorithms are to mimicry or inspiration. What are the biological roots and operators used? What are the key similarities and mathematical differences between two bio-inspired algorithms apart from the terminology used?
To help ensure that future bio-inspired algorithms do not recycle the same concepts, this paper categorises the current state of the art in Evolutionary Computation under a biological framework. The framework can show how current algorithms relate to each other and demonstrate gaps in the evolutionary synthesis that computational algorithms have yet to explore.

2. Moving towards an extended evolutionary synthesis

Despite the range of available algorithms, Evolutionary Algorithms can be closely linked to a relatively small part of the evolutionary literature, focused on genetic inheritance and the Modern Synthesis (Figure 1). Swarm Intelligence is also linked only to the cultural inheritance concepts of the extended synthesis. While the mechanisms from the Darwinian concepts and the Modern Synthesis have all been included in Evolutionary Computation, there is limited inspiration taken from the Extended Evolutionary Synthesis.

The elements of the Extended Evolutionary Synthesis expand on the existing concepts of the Modern Synthesis to allow for a broader range of ideas and explanations [9, 10]. These concepts give further explanations for how biological organisms can adapt and change to the environment quickly compared to natural selection, that can’t be explained purely through the original concept developed by Mendel and Darwin. In the Modern Synthesis, phenotypic variation is seen as random based on genetic variation and inheritance. Natural selection then applies the environmental pressure to determine the fitness of different individuals and species. In the Extended Evolutionary Synthesis, it is argued that phenotypic variation can be guided rather than random, allowing organisms to combat selection pressures with fast adaptive variations to prevailing environmental conditions. For example, evolutionary developmental biology (evo-devo) bridges the gap between developmental biology and evolutionary biology [13], providing an understanding for how individual development occurs, and how the developmental process directs phenotypic variation in individuals with the same genotype. As another example, niche construction relates to ecological inheritance and is the process in which individuals change the environmental state to better suit their phenotypic properties [14].

The different forms of non-genetic inheritance can be divided based on their mode of transmission [15]:

- **Epigenetic inheritance** - In genetic inheritance, the evolution of species comes from changes in the DNA sequence due to natural selection. Epigenetic mechanisms alter the DNA expression without adapting the DNA sequence [16]. This allows for a rapid change in phenotypes without a change in the inherited genotype, leading to faster adaptation to selection pressures. Epigenetic marks, markers in the DNA sequence to alter the expression of genes, trigger changes in an individual’s phenotype based on external factors such as the environment, and are passed on from parent to offspring. While epigenetic marks can cause changes to a phenotype, they can also remain dormant awaiting triggering by an appropriate environmental cue. This is a crucial difference between epigenetic and genetic inheritance. Traits transmitted through genetics are considered much harder to change or revert compared to epigenetics.

- **Cultural inheritance** - Apart from inherited genotypes, information relevant to survival can also be exchanged and inherited socially. Cultures themselves can also “evolve” [17] and can be found in a large number of animal species. A trait is at least partially culturally inherited if it follows the following four criteria [18]:
  1. The trait is expressed as a result of learning from other individuals, and not inherited in another way.
  2. The trait must be passed on through multiple generations. This allows socially learned traits to become a part of evolution, as transmission across the same generation will not lead to inheritance.
  3. The phenotype of an individual must be changed as a result of social learning for long enough to allow new individuals to observe and learn the same trait.
4. Changes to the individual’s phenotype must be general and adaptable to other similar conditions.

- **Ecological inheritance** - Darwin [19], observed that individuals can alter their surrounding environment to improve their chances of survival. Examples of this are dams and nests made by animals that can sometimes be passed on to future generations. This can be both an in-generational, parent generation to parent generation, and trans-generational effect, parent generation to offspring generation, depending on whether the ecological changes made by one generation last for the next generation’s benefit.

- **Parental effects** - Parents can often have an effect on their offspring’s phenotype during the developmental stages of the offspring’s life. Parental effects are most often defined as the effect of parents on their offspring phenotype over and above the offspring’s genotype. For example, some birds put antibodies into their eggs’ yolk to defend their offspring from disease [20]. Parental effects can also occur indirectly, for example in offspring seeds affected by the maternal light environment gaining enhanced fitness [21]. This directly affects the offspring’s phenotype independent of their genotype; this is a trans-generational effect.

- **Evolvability** - The capacity for an organism to adaptively evolve [22]. Within contemporary evolutionary biology, the concept takes many varied definitions, but, in algorithms, it is represented by hyper-parameter choices. The choice of mutation rate, population size, crossover method all affect the evolvability of the generated populations. Some algorithms such as CMA-ES (Covariance Matrix Adaptation Evolution Strategy) [23] and SHADE (Success-History based Parameter Adaptation for Differential Evolution) [24] introduce additional parameters and memory to dynamically evolve hyper-parameter choices and increase robustness to poor initial hyper-parameters. Evolvability also relates to genomic evolution, the evolution of genome architecture itself, with evolvability being the capacity to allow this form of evolution to occur. Computationally, this is related to how variables and solutions to problems are structured.

3. Relating current bio-inspired algorithms to the Modern Extended Evolutionary Synthesis

In Evolutionary Computation, the literature is divided between two general fields:

- **Evolutionary Algorithms** [25] (EC) - Algorithms with a foundation in genetics, these date back to Turing’s learning machine [26], and include the branches of Evolutionary Programming (EP), Evolution Strategies (ES), and Genetic Algorithms (GA). These algorithms generally involve the genetic mechanisms of selection, recombination (crossover) and mutation.

- **Swarm Intelligence** [27] (SI) - Algorithms based on collective intelligence with patterns of communication and interaction in a population. Swarm Intelligence algorithms cover a wide range of biological inspirations, from animal behaviour algorithms such as Particle Swarm Optimisation [28] (PSO) and Ant Colony Optimisation [29] (ACO) as well as more esoteric inspirations such as political anarchy (Anarchic Society Optimisation [30]).

In Evolutionary Algorithms, individuals are presented as a genotype that evolves with genetic operators. The algorithms use genetic operators to represent candidate solutions as genotypes and the genetic mechanisms evolve the genotype through genetic inheritance. Conversely, individuals in Swarm Intelligence algorithms are typically presented as phenotypes, which are an organism’s observable traits such as physical appearance or behaviour. Phenotypes are the target for selection, for example bigger horns, whereas genotypes represent the response to selection. These phenotypes are often used in metaphors to hunting, foraging, and movement behaviour, with few genetic components. The focus of the Extended Evolutionary Synthesis is that there are many interacting routes that influence the final phenotype, not only genetic inheritance, as encoded in EAs, or within-generation cultural transmission, as encoded in SI, but rather a mix of influences both within and across generations. This diversity of influences reduces reliance on a single mode of inheritance and generates phenotypes from a diversified portfolio of influences.
against maladaptations while also providing more rapid adaptation when genetic, indirect genetic, and phenotypic effects align [10].

Using a biological framework for information transmission [31], Figure 2 shows how the genetic and cultural sources of information are closely linked to Evolutionary Algorithms and Swarm Intelligence respectively. The mechanisms further right leverage non-genetic transmission more than those on the left. Evolutionary Algorithms are mostly based on the genetic source while Swarm Intelligence methods are based on the cultural source. Phenotypic plasticity is the ability for the same genotype to produce different phenotypes in response to epigenetic or environmental conditions [32]. On the far left, genetic inheritance has low plasticity as genotypes take many generations to mutate and evolve. Genetic inheritance by itself cannot react to sudden changes to the environment and adapt the genotype immediately. Cultural and non-transmitted information can lead to higher phenotypic plasticity, higher variation, in nature as adaptation can occur quickly within a few generations. On the far right, non-transmitted information is information that is not inherited by future generations; this information has the highest plasticity as it can act immediately on environmental changes, but is unstable and does not carry forward to future generations. Non-transmitted information is included in some algorithms that utilise a population of individuals acting with a certain behaviour that does not require interaction with other individuals. For example, the Bat Algorithm [33] is inspired by the echolocation techniques of bats. The individual bats interact with the environment to locate prey, but do not transmit information with each other.

The categories of parental and ecological inheritance are omitted for simplicity from Figure 2 as they can be argued as a higher level of cultural inheritance from a computational perspective. For example, niche construction [34] is the concept of changing the environment to better suit the development of future generations. These changes become a part of evolution when they affect natural selection, such as burrows and nests defending family units or otherwise less fit organisms. However, niche construction can be seen as a form of cultural inheritance where the trait for creating ecological change in the environment is passed down through social learning. Similarly, parental effects can be classed as part of cultural inheritance. Parental behaviour, which affects the offspring phenotype, can be passed on through social learning, either in-generational or trans-generational.

### 4. Categorising algorithms

Table 2 breaks down each category of inheritance into the biological concepts defined in Table 1 to show the overlap between the selected algorithms. The algorithms were chosen if they were popular within the Evolutionary Algorithm and Swarm Intelligence fields, defined as more than 1000 citations, or if they showed strong performance in recent benchmarking studies [Appendix A]. There is a split between Evolutionary Algorithms, which all use selection, recombination, and mutation operators, and Swarm Intelligence algorithms, which have a mix between specialised roles for individuals and different forms of social learning and communication. While most of the algorithms fit neatly into genetic or cultural information sharing, contrasting with evolutionary theory where multiple mechanisms act together, there are a few algorithms that use a spread of information mechanisms: cMLSGA uses specialised roles and social learning, while GB-ABC and Firefly Algorithm utilise elements of selection; GB-ABC and EBO/CMAR use recombination; HEIA uses co-evolution to spread social learning; and Cuckoo Search uses genetically modified nests with crossover and mutation operators. The introduction of multiple mechanisms has recently proven to balance convergence and diversity, with cMLSGA and HEIS showing top performance on state-of-the-art multi-objective benchmarking problems [2], and EBO/CMAR shows top performance in a CEC’17 Single Objective Bound Constrained competition [35], an area normally dominated by variants of GAs and DE algorithms.
Table 1: Biological categories of transmission for different levels of evolution.

| Category      | Sub-category        | Description                                                                                                                                                                                                 |
|---------------|---------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Genetic       | Selection           | In each generation, a subset of the population is chosen to reproduce the next generation. In biological terms, this relates to the survival of the fittest. Individuals with fitter genes are typically able to live longer and produce more offspring. In computational terms, individuals are selected based on their fitness against the objective function. |
|               | Recombination       | Also called crossover, when two individuals produce offspring, genetic material from both parents are used. This can be in a sexual or asexual way. This results in offspring that share some attributes with both parents. Crossover affects both diversity, avoiding in-breeding depression, and convergence of the population as it creates new combinations while keeping the same base genetic material from its parents. |
|               | Mutation            | When offspring are formed, mutation can occur. These mutations could be neutral, beneficial or detrimental to the survival of that individual. Mutation helps improve diversity by producing genetic material that has not been explored before by the population. |
| Epigenetic    | Mitotic             | The transmission of epigenetic changes through mitotic cell divisions. Epigenetic marks cause variations to occur in an individual which are propagated through cell divisions when the marks are triggered as a response to environmental cues. Mitotic epigenetic inheritance only transfers the epigenetic changes across the same generation. |
|               | Germline            | Epigenetic changes caused by environmental factors in the parent are passed down to the offspring and to further generations [35]. This affects individuals across multiple generations, even if the environmental factor that triggered the change only happened during the first generation. |
|               | Experience-dependent| Epigenetic marks that influence parental behaviour causing the same epigenetic mark to appear in the offspring generation. The marks can persist across multiple generations, but the transmission can also be broken when environmental factors cause one generation to stop the same parental behaviour. For example, maternal behaviour in rodents cause the offspring to exhibit the same behaviour as their offspring. But if there is a break in one generation where the maternal behaviour does not occur, the epigenetic transmission stops [36]. |
| Cultural      | Specialised roles   | Individuals in a population have different roles to fulfil. For example, scout and guard bees in a colony, or mongooses that form foraging niches [37] due to competition within the population. In some cases, specialised roles are formed and last through multiple generations, as in the case of ants and bees. In others such as the mongooses, the specialised roles may only form in a particular generation due to external factors during the generation’s lifespan. |
|               | Social learning (individual level) | Individuals learning from other individuals in the population through direct information sharing, teaching, environmental stimulus or imitation and emulation of other individuals. |
|               | Social learning (population level) | Information transfer between populations (cultures) where different populations may have different variations in behaviour as a result of social learning. |
Figure 2: Sources of information transmission for phenotypic variation linked to inspiration for bio-inspired algorithms adapted from [31].
Table 2: How bio-inspired algorithms fit into a biological framework for different forms of inheritance.

| Algorithm category | Algorithm          | Genetic | Epigenetic | Cultural |
|--------------------|--------------------|---------|------------|----------|
|                    |                    | Selection | Recombination | Mutation | Mitotic | Germline | Experience-dependent | Specialised roles | Social learning (individual) | Social learning (population) |
| Genetic Algorithm  | NSGA-II            | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | MOEA/D             | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | HEIA               | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | cMLSGA             | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
| Evolution Strategies Differential Evolution | CMA-ES | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | SHADE              | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
| Swarm Intelligence | CLPSO              | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | SMPSO              | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | ACO                | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | ABC                | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | GB-ABC             | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | GWO                | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | EBO with CMAR      | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | Firefly Algorithm  | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |
|                    | Cuckoo Search      | ✓        | ✓          | ✓         |         |          |                    | ✓                    |                        |                        |

* Cuckoo Search variants (Cuckoo-GRN and Modified Cuckoo Search) include additional genetic and cultural mechanisms respectively.

NSGA-II: Non-dominated Sorting Genetic Algorithm II
MOEA/D: Multiobjective Evolutionary Algorithm Based on Decomposition
HEIA: Hybrid Evolutionary Immune Algorithm
cMLSGA: Co-evolutionary Multilevel Selection Genetic Algorithm
CMA-ES: Covariance Matrix Adaptation Evolution Strategy
SHADE: Success-History based Parameter Adaptation for Differential Evolution
CLPSO: Comprehensive Learning Particle Swarm Optimisation
SMPSO: Speed-constrained Multi-objective Particle Swarm Optimisation
ACO: Ant Colony Optimisation
ABC: Artificial Bee Colony
GB-ABC: Artificial Bee Colony Algorithm Based on Genetic Operators
GWO: Grey Wolf Optimiser
EBO with CMAR: Effective Butterfly Optimiser with Covariance Matrix Adapted Retreat Phase
While some existing studies \cite{39, 40, 41} investigate the use of epigenetics in Evolutionary Computation, neither their performance nor popularity fit the criteria to be included in this discussion. It is proposed that this is because they do not capture the inheritance and transfer of epigenetic information to future generations, and so miss out the adaptability and reversibility of epigenetics. A discussion on the key concepts of epigenetics and why these studies miss these concepts is presented in section \ref{section:epigenetics}. A justification of Table \ref{table:epigenetics} is given in the following subsections.

### 4. Genetic algorithms

Genetic Algorithms (GA) are inspired by natural selection, evolving a population of potential solutions towards an optimal solution. They are tightly linked to a simplified concept of genetic evolution using selection, crossover and mutation mechanics. The focus in development is almost entirely related to different selection mechanisms, with only a small number of modern crossover and mutation mechanisms preferred, which are no longer bio-inspired. In addition to these operators, many GAs also incorporate other mechanics such as elitism \cite{42} as a representation of “survival of the fittest”; which keeps the best individuals in a population, copying them directly into the next generation to improve convergence at the cost of diversity. This provides a considerable computational benefit and ensures that the fittest solution can’t be lost over the generations.

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#### 4.1.1. Niching GAs

The NSGA-II \cite{43} algorithm belongs to a family of niching algorithms, where the most popular versions are NSGA-II and its refinement NSGA-III \cite{44}, which is an extension for many-objective problems. The difference between this approach and other Genetic Algorithms is the use of non-dominated sorting to rank individuals for selection but it also uses a density estimator to maintain diversity in the population. The density estimation is not a genetic operator, as it does not involve the genotype of candidate solutions; it is not epigenetic as it is not inherited between individuals, and it is not cultural as it is not learned through interaction between individuals, rather it is forced upon the population as an external system to ensure individuals are spread out along the Pareto front. As such it uses computational elements to improve selection but still incorporates selection, recombination, and mutation.

#### 4.1.2. Decomposition based GAs

MOEA/D \cite{45} is a GA approach that utilises mathematical decomposition to split a multi-objective problem into a number of sub-problems with an assigned weight vector. The population is split to solve each sub-problem separately, where each individual can only reproduce with individuals within the same neighbourhood. Although the population is divided into sub-populations and reproduction between neighbourhoods of sub-populations is allowed, there is no learning or interaction between individuals for social learning and this boosts exploitation of the search but reduces the exploration. Many variants of the original MOEA/D algorithm focus on improving different aspects of the original algorithm such as the decomposition method \cite{46, 47} or weight vector generation \cite{48, 49}. Compared to other approaches the development of MOEA/D focuses on mathematical methods for selection but still incorporates selection, recombination, and mutation.

#### 4.1.3. Co-evolutionary GAs

Co-evolutionary GAs use cooperation or competition between two populations or algorithms to find the best solutions. These have been gaining more popularity in the Evolutionary Computation literature, with papers proposing that co-evolution creates a generalist approach which reduces hyperparameter tuning \cite{4}. The top performing method is a hybrid co-evolutionary method HEIA \cite{50} that also uses sub-populations, but instead of dividing based on decomposition of the problem, the sub-populations use different algorithms for evolution, representing different selective regimes. After each generation, the best individuals from each sub-population are saved in an external archive and the sub-populations are cloned for the next generation with an Immune Algorithm. With this co-evolutionary approach, the sub-populations can naturally develop specialised roles to solve the problem. This means the algorithm incorporates selection, recombination, mutation and specialised roles, but with a focus on exploration of the space.
4.1.4. Multilevel selection

Multilevel Selection is the idea that natural selection occurs at different levels such as the genetic level \[51\], the individual organism level \[52\] or the species level. The existence of altruism, a phenotype that contributes to group advantage at the cost of disadvantaging itself \[53\], suggests that a disadvantage at one hierarchical level may be an advantage at another level, justifying why we see this behaviour. It does not fit into the epigenetic and cultural concepts of non-genetic inheritance but is another concept in the Extended Evolutionary Synthesis. MLSGA \[54\] uses the idea of multilevel selection by evolving on both an individual level and sub-population level (collectives). Co-evolutionary mechanics were further included in cMLSGA \[2\] to allow different evolutionary algorithms for the individuals of different sub-populations, allowing collective co-evolution which increases the generality of the algorithm. The sub-populations are groups based on similarities between individuals, allowing specialised roles to be formed. Further, at the sub-population level, evolution can be seen as a form of social learning at the population level, where information is transferred between the sub-populations. This means the algorithm incorporates selection, recombination, mutation, specialised roles, and social learning at the population level.

4.2. Evolution strategies

Evolution Strategies \[55\] use the mechanics of selection, recombination and mutation to evolve the population. However, unlike traditional GAs, Evolution Strategies are self-adapting with a distinct set of endogenous and exogenous parameters \[56\]. Endogenous parameters are evolved along with an individual solution and passed down to offspring individuals, independent of others in the population. This contrasts with GAs where all parameters such as crossover and mutation rate are set beforehand, making them all exogenous. Endogenous parameters control the strategy of ES algorithms by changing the statistical properties for mutation. There are two steps of recombination and mutation for an individual \(i\) in each generation:

- recombination to form the endogenous strategy parameters \(s(i)\)
- recombination to form the solution variables \(y(i)\)
- mutation of the strategy parameters
- mutation of the solution variables using the strategy parameters

CMA-ES \[23\] is an improvement to the traditional ES algorithm. It uses a covariance matrix to generate its mutation distribution that is adaptive and evolves with the search. This allows the strategy parameters to adapt more closely during local search. The parameters are adapted based on statistics gathered through previous generations. The self-adaptive endogenous parameters can be seen as a form of evolvability, in the sense that the capacity to evolve also changes \[22\]. The mechanism of passing down and evolving this extra set of parameters changes the capacity of evolution in the population, as the mutation rate is changed and adapted based on previous generations. As evolvability is similar to tuning hyperparameters, the use of a set of self-adapting parameters to control mutation automates tuning of the mutation rate. As such it uses selection, recombination and mutation, alongside some elements of evolvability.

4.3. Differential evolution

Differential evolution \[57\] (DE) is another branch of evolutionary computation that is similar to genetic algorithms. Selection, recombination and mutation operators are all used in DE. The main difference between GAs and DE algorithms is the representation of the individual. DE uses real value vectors and their recombination and mutation operators revolve around the difference between two vectors.

A popular variant to the DE algorithm, the Success-History Adaptive DE \[24\] (SHADE) adapts the scaling factor and crossover rate parameters dynamically by changing them based on a memorised history of successful parameters in previous generations. The parameters are changed for each individual, rather than as a whole population. This is similar to social learning where successful parameters from other individuals are used to evolve the parameter selection for new individuals. This additional memory is also stored through multiple generations for robustness, so a poor set
of parameters in one generation does not negatively impact the rest of the search. As such it uses
computational elements to improve selection, recombination and mutation alongside some cultural
elements of social learning.

4.4. Swarm Intelligence

In contrast to evolutionary algorithms, swarm intelligence algorithms focus on collective behaviour
and the transfer of information across the population. Typically a single generation is used and
the population traverses the search space with different mechanics analogous to different behaviour
in animals. Some algorithms also include additional genetic components such as GB-ABC \cite{58}, an
Artificial Bee Colony algorithm Based on Genetic Operators.

4.4.1. Particle swarm optimisation

Particle Swarm Optimisation (PSO) is an algorithm developed in 1995 by Eberhart and Kennedy
\cite{28} for optimising nonlinear functions. The algorithm is based on the concept of social behaviour
and sharing information. A population of particles represents potential solutions in the search
space, at each iteration, each particle updates its velocity and position. The velocity update is
based on a combination of the best position found so far by the particle, and the best position found
so far by the entire swarm. This is an example of social learning, as the velocity is determined by
the best solution found by an individual, but also by the best solution found so far by the entire
swarm.

The Comprehensive Learning Particle Swarm Optimiser \cite{59} (CLPSO) extends the idea of social
learning. Rather than basing the velocity on the single best solution found so far, CLPSO in-
corporates all other particles in the swarm during the velocity update to increase diversity. The
algorithm was able to show significant improvements to performance, especially to multimodal
problems. The PSO is based solely on social learning at the individual level whereas CLPSO
extends this to the population level.

A successful PSO algorithm for multi-objective problems is the Speed-constrained Multi-objective
PSO \cite{60} which uses the concepts of Pareto dominance and a nearest neighbour density estimator
to select leaders. The velocity of particles is also limited to disallow extreme values. The algorithm
is based on social learning like other PSO algorithms, but with an added element of selection to
choose leading particles.

4.4.2. Ant Colony Optimisation

Ant Colony Optimisation (ACO) simulates a population of ants that moves through the search
space probabilistically based on pheromone trails left behind by previous generations. Pheromone
values decrease with each iteration so that old trails fade and new ones form as the search space
is explored. Some pheromone trails will be reinforced if the next generations continue to follow
the same path, leading to higher pheromone values, which are associated with better solutions.
Although ACO uses multiple iterations/generations, there is no information transfer through ge-
netic inheritance. The individuals in the previous generation leave behind ecological signals with
pheromone trails that affect the behaviour of new generations, but there are no genetic operators
in use. This can be seen as ecological inheritance, which has been defined here as part of social
learning. The use of pheromone trails is core to the concept of ACO. Popular ACO algorithms
such as the Max-Min Ant System \cite{61} (MMAS) and the Continuous Orthogonal Ant Colony \cite{62}
(COAC) focus on improving the mechanics of the pheromone trails. MMAS limits the maximum
and minimum pheromone values on the trails to avoid stagnation. COAC uses orthogonal design
to split up the search space into regions for fast exploration. This was shown to improve the con-
vergence speed for continuous unimodal problems, finding the optimal solution in less than half the
number of function evaluations, at the cost of convergence speed for multimodal problems. The
ACO is based on social learning at the individual level and specialised roles.

4.4.3. Artificial Bee Colony

In an Artificial Bee Colony \cite{63} (ABC), the population is split into three different types of bees:
employed bees, onlooker bees and scout bees;
• employed bees search for better food sources in their local neighbourhood and share that information to onlooker bees in the region. They are able to remember new food sources if they are better than an existing food source in its memory.

• Onlooker bees take the information given by employed bees and move towards new food sources based on the information.

• Scout bees search for new food sources randomly without taking into account any information. They become employed bees when a new food source is found.

The three types of bees carry out different roles depending on their proximity to food sources. Scout bees carry out the exploration phase of the search by moving randomly while employed bees carry out an exploitative search by searching locally for better food sources. Social learning can also be observed as the bees change behaviour based on information from other bees and contextual clues from the environment. The role of an individual bee is not static, for example onlooker bees become employed bees after analysing the information received from other employed bees. Similarly, employed bees become scouts when their food source is exhausted. Some variants on the ABC algorithm include genetic operators (GB-ABC [58]) to improve global and local search for binary optimisation problems. The ABC algorithm uses both specialised roles and social learning between individuals with the GB-ABC variant including genetic operators.

4.4.4. Grey Wolf Optimiser

The Grey Wolf Optimizer (GWO) [64] is an algorithm inspired by grey wolf social structure and hunting techniques. It mimics a leadership hierarchy with four types of grey wolves, alpha, beta, delta, and omega. During a search, the alpha, beta, and delta wolves are the three best solutions found so far. All other individuals update their position according to the positions of the alpha, beta, and delta wolves. Figure 3 shows how an omega wolf’s position is updated based on the positions of the alpha, beta and delta wolves. Two coefficient vectors $A$ and $C$ are used to fluctuate between exploration, searching for prey, and exploitation, attacking the prey. When $|A| > 1$ the wolves diverge from the prey instead of moving towards it. Similarly, $|C| > 1$ emphasises attacking the prey so the wolves move faster towards it while $|C| < 1$ de-emphasises attacking.

There is a use of specialised roles among the wolf pack to form the hierarchy and social learning occurs during a hunt, when the omega wolves follow the alpha, beta and delta wolves for direction. Information exchange between the wolves is used as the omega wolves move to position themselves based on the positions of the wolves higher up in the hierarchy. The GWO algorithm uses both specialised roles and social learning between individuals.
4.4.5. Butterfly Optimiser

Butterfly Optimiser [65] (BO) aims to simulate the mating behaviour of butterflies. It splits a population of butterfly individuals into two groups, males and auxiliary butterflies in different specialised roles. The male butterflies operate in either perching or patrolling behaviour for exploitation and exploration of the search space respectively. Male butterflies learn and follow auxiliary butterflies to better positions as a form of social learning. This allows for faster exploration of the search space, as auxiliary butterflies can continue to explore when some males decide to perch. The attractiveness of a location affects the probability that a male butterfly goes into perching behaviour at that location. This is an environmental factor affecting the individual’s behaviour similar to an epigenetic effect, but because there is only a single generation, such behavioural effects are not passed down and therefore the algorithm is not epigenetic.

An improved variant of Butterfly Algorithm, Effective Butterfly Optimiser with Covariance Matrix Adapted Retreat Phase [66] (EBO/CMAR) uses a crossover operator to increase diversity and a retreat phase on a third group of butterflies to improve convergence during local search. After each iteration information is exchanged between each group of butterflies to replace the worst individuals in one group with the best individuals from another. This is social learning on a population level, as each group of butterflies uses different behaviour and the best individuals from other groups can be learned from. The BO uses both specialised roles and social learning between individuals with the EBO/CMAR using genetic operators to improve the performance.

4.4.6. Firefly Algorithm

The Firefly Algorithm [67, 68] (FA) is based on the flashing patterns and behaviour of fireflies. The firefly individuals are attracted to each other proportional to their brightness (fitness) and the distance between two individual fireflies. Dimmer (less fit) individuals then move towards the brighter (more fit) individuals. A firefly’s brightness is determined by the landscape of the objective function. This means their fitness is related to an individual’s phenotype rather than their genotype. This uses elements of selection, as fireflies are more attracted to bright individuals. Social learning is also observed, as an individual moving towards brighter fireflies becomes brighter themselves.

4.4.7. Cuckoo Search

Cuckoo Search [69] is an algorithm inspired by the aggressive egg laying behaviour of cuckoo birds, which lay eggs in the nests of other birds. The algorithm uses the concept of Levy flights [70] to create a random walk for the population. Eggs laid in nests represent solutions. In each iteration there is a probability for the cuckoo eggs to be thrown out or the nest abandoned by the host birds as a selection mechanism. In biological mechanisms, Cuckoo Search only uses selection. However, improvements to the algorithm were made by adding either a genetic or cultural component. In Cuckoo-GRN (Cuckoo Search with Genetically Replaced Nests) [71] the convergence of the algorithm was improved by replacing abandoned nests with crossover and mutation genetic operators. This leads to faster convergence as new nests were created genetically using existing nests with high fitness. Another variant, MCS (Modified Cuckoo Search) [72] adds a cultural mechanism instead of a genetic mechanism. When new eggs are generated, information is exchanged between a fraction of eggs with the best fitness. New eggs are then generated in midpoint positions between the two chosen eggs. The additional information sharing also improves convergence compared to the original Cuckoo Search. These two variations demonstrate how the addition of simple biological mechanisms helps improve performance of an algorithm.

4.5. Summary of current algorithms in a biological framework

Figure 4 categorises the mechanisms of the main families of Evolutionary Algorithms and Swarm Intelligence under either genetic, epigenetic or cultural information transfer, using a single algorithm to represent each family. In general, most of the categories of algorithm use a single category of information transfer, the Evolutionary Algorithms focus on different forms of genetic transfer with mechanisms focused around changing the selection of the population to mate and Swarm Intelligence focuses on different forms of cultural information transfer. There are currently no
successful epigenetic mechanisms, despite it’s importance in describing the process of evolution. Many of the popular Evolutionary Algorithms such as NSGA-II [43], MOEA/D [15], and SHADE [24] have diverged from their biological roots into mathematical or statistical methods.

However, there are algorithms that show some overlap between genetic and cultural mechanisms, which can be seen for both Evolutionary Algorithms and Swarm Intelligence algorithms. For example, cMLSGA uses multilevel selection by evolving both the individuals and the collectives of individuals, and GB-ABC [58] adds genetic operators to the bee colony algorithm. The mechanisms resulted in increased diversity for cMLSGA and increased convergence for GB-ABC. The main gap is in epigenetic transfer with only EBO/CMAR (Effective Butterfly Optimiser with Covariance Matrix Adapted Retreat Phase), using elements of this type of information transfer but which still can’t be considered to be fully epigenetic. The environmental trigger to change the behaviour is similar to an epigenetic mark, but is missing the ability to be passed on and evolve in future generations. There are other algorithms that aim to incorporate epigenetic mechanisms but do not meet the criteria of high citation count or high performance in benchmarks. These algorithms will be discussed next.

Figure 4: How bio-inspired algorithms fit into biological sources for phenotypic variation.

5. Missing concepts from the Extended Evolutionary Synthesis

A few elements from the extended evolutionary synthesis have been explored in successful algorithms: Swarm Intelligence algorithms fit closely to the concepts of cultural inheritance and information transfer; cMLSGA has been shown to be a successful implementation of multilevel selection; Evolvability is represented by hyper-parameter choices, which algorithms such as CMA-ES dynamically alter during a search. Returning to the biological concepts in Figure 1 this leaves evo-devo theory, niche construction, epigenetic inheritance, plasticity, and genomic evolution yet to be explored. The improved performance of algorithms such as EBO with CMAR, Cuckoo-GRN,
GB-ABC, and co-evolutionary methods show that a merge of multiple evolutionary techniques can have potential benefits.

While the extended synthesis provides a number of opportunities, not all of the elements provide easy inspiration for practical optimisation problems. Evolutionary and developmental biology (Evo-devo) includes the developmental stages of living organisms and the evolution of developmental processes. While in some ways most closely replicating the initial vision proposed by Turing [26] of generating a child and teaching it to learn, adapting the concept for general evolutionary algorithms would require substantial expansion of the simple genotype model of evolution used in evolutionary algorithms, such as including properties relating to gene regulation, homeobox genes and allometry. Evo-devo provides a number of developmental steps for fine tuning an organism, but in the algorithmic world this is unnecessary when more generations can be run instead. It is possible to apply evo-devo specific applications, such as digital architectures [73], where domain-specific concepts in architecture can be linked to evo-devo processes, and the time taken to generate solutions means a lower number of generations can be run. Similarly, genomic evolution involves the evolution of genome architecture itself. In computational terms, genomic evolution would involve the evolution of the number of variables or range of values in an optimisation problem. These values are typically set based on the problem and do not require evolutionary mechanics applied to them.

Niche construction requires individuals in the population to alter and change their own environment to suit the population’s properties. This allows populations and genes that are normally less fit under the environment to gain fitness due to the changes made to the environment, but this is difficult to accomplish computationally. Optimisation problems are usually predefined and the fitness landscape is dependent on the problem. If an algorithm is able to change the fitness landscape to suit the solutions it produces, it changes the problem definition, meaning the solutions found may no longer be applicable or useful to the original problem.

However, there are a range of unused mechanisms which can be considered to provide excellent bio-inspiration for a new range of algorithms, documented in the following subsections.

5.1. Epigenetics

Epigenetics plays an important role in adapting a population to new conditions and environments quickly. In computational terms, epigenetic mechanisms should help to improve convergence, potentially spreading changes through a population faster than genetic evolution, and improve stability around a solution in the face of environmental changes. There are a number of different epigenetics processes such as DNA methylation, bookmarking, gene silencing, gene repression, and genomic imprinting that are triggered by different factors such as environment, diet, or the presence of certain chemical compounds [74].

In the Modern Synthesis view of evolution, genetic changes occur randomly and fitness is guided by natural selection. Similar to this, the development of modern genetic algorithms focus on improving the selection process while keeping genetic changes random to retain diversity. This requires a number of generations for suitable traits with high fitness to spread throughout a population, even with mechanisms such as elitism. Epigenetic inheritance allows for faster changes based on environmental cues which can occur simultaneously among multiple individuals in the same generation. These adaptive adjustments also do not affect the underlying genotype, allowing regular genetic processes to occur and epigenetic processes to be reversed. The inheritance of epigenetic tags in parallel with genetic inheritance results in continual rapid changes with a diverse set of tags among a population, without disrupting underlying genetic processes [75]. This is an important aspect in evolutionary biology to guide phenotypic variation in a direction suitable for the environment instead of relying solely on random mutation and natural selection.

5.2. Phenotypic plasticity

The concept of phenotypic plasticity is the idea that an organism’s behaviour or physiology could change due to environmental factors [76]. The class of optimisation problems that focuses on dynamic problems, where the objectives and constraints may be unstable and change throughout
the search, would be suitable for algorithms with flexible, plastic responses. Algorithms in Swarm Intelligence can exhibit some of this behaviour, for example when new bees take different roles in the Artificial Bee Colony depending on the number of existing bees in other roles. However, there is no scale or range of plastic responses in reaction to a changing environment in the ABC implementation.

6. Opportunities to include epigenetic mechanisms in evolutionary algorithms

6.1. Existing studies

The key concept of epigenetics is to allow for fast variation when appropriate. Existing studies [39, 40, 41] inspired by epigenetics are currently missing the key feature of triggering mechanisms based on the fitness of the population to the environment. They often trigger the mechanism probabilistically without any distinction between individuals, parents and how the epigenetic marks are passed on. This probabilistic method is more akin to bet hedging [77] than epigenetics, where the mechanics do not improve individual fitness in stationary conditions with no drastic changes in the environment, but create advantages in extreme conditions such as being stuck at a local optima.

An epigenetic algorithm based on intra-generational epigenetic processes used by bio-molecules is developed by Periyasamy [39]. This system mimics cellular organisation, with individuals of bio-molecules performing independent tasks in a swarm-like manner, and require specific conditions to be met. The focus on the epigenetic processes uses no genetic operators, which misses a genetic component to contribute to the final phenotype. So while the use of epigenetics can improve the convergence of this algorithm, it potentially loses diversity from the lack of genetics and can get stuck at local optima.

The epigenetic process of cytosine methylation is incorporated into a Genetic Algorithm to solve the Knapsack problem [40]. Cytosine methylation blocks a part of an individual’s genotype during the crossover operation. Figure 5 shows the methylation operation used in reproduction, where a portion of the crossover from parent 1 is blocked. This aims to transfer a larger portion of the fitter parent’s genotype while silencing the poorer parent. This constant probability for methylation to occur means the epigenetic tags are assumed to always be passed to new generations without any dynamic changes to external factors.

Finally, the concept of methylation and gene silencing is incorporated into an epiGenetic Algorithm (epiGA) [41]. Similar to [40], a number of parent genes may be masked based on the probability of the epigenetics mechanism occurring. The constant probability of trigger for the epigenetic process is assumed to always be passed to new generations without any dynamic changes to external factors.

Figure 5: Concept of the cytosine methylation epigenetic process used in [40], where part of the parent genotype is blocked by the epigenetic process.
mark means the marks do not evolve or change through new generations. The occurrence of the epigenetic trait is probabilistic, so it occurs with some chance rather than being triggered due to environmental or parental cues. This misses the concept of allowing fast variation when appropriate. So, while some algorithms are inspired by epigenetics they are currently missing the key features that lead to the benefits seen in evolution. These features are outlined in the following subsections.

6.2. Epigenetic tags - the epigenotype

A key aspect existing studies do not capture is the inheritance and transfer of epigenetic information to future generations. While the epigenetic mechanisms implemented were accurate, this transfer is important as it guides the direction of phenotypic change. Without this aspect, the epigenetic mechanisms simply act as another form of mutation, probabilistically switching genes on and off. To include the epigenetic information transfer, epigenetic tags can be used to form an epigenotype \cite{78}, to keep a history of inherited epigenetic changes and allow changes to an individual’s genotype to be triggered based on these tags. Epigenetic tags can be added and removed based on signals from the environment, or based on inheritance and crossover operations when forming offspring individuals \cite{79}. Epigenetic tags can also help control gene expression in response to environmental changes. In biology this helps to form “memory” based on changing environments \cite{80}. The memory of the recent environment allows for fast adaptation and stability. By controlling how genes are expressed using an epigenotype, suitable traits are constantly adjusted to improve fitness before longer term genetic changes can be applied.

Computationally, each variable in a solution can contain a set of tags that can be inherited and modified. Figure 6 shows the epigenetic tags on top of some variables in the genotype. The tag can be used to encode mechanisms to alter the variable after genetic operators are applied. These mechanisms can then help increase convergence by guiding phenotypic variation in a direction matching selection pressures. The underlying genetic mechanisms are further unaffected by epigenetic changes, and epigenetic changes can be easily reversed, reducing the cost of poor mutations compared to genetic mutations.

The epigenotype represents the three key aspects of epigenetics:

- the transfer of epigenetic information,
- self-adaptability to environmental changes,
- fast convergence from direction variation.

These aspects may have potential benefits especially for dynamic problems where the Pareto front is not static. The self-adaptability and fast convergence would allow algorithms with an epigenotype to adjust to a changing Pareto front quickly.

6.3. Epigenetic mechanisms

With the use of an epigenotype \cite{78}, epigenetic tags can be added, removed, and inherited to future generations. An epigenotype alters the phenotype without changes to the underlying phenotype.
The tags can then be used to encode different epigenetic mechanisms to be triggered. The mechanisms have a range of effects on the genotype, such as switching genes on and off, or reducing gene expression based on the location and number of tags in the epigenotype.

### 6.3.1. Genomic imprinting

Genomic imprinting [81] restricts the expression of a gene to one parent. Imprinting is useful when the imprinted alleles lead to different phenotypes that affect an individual’s fitness. This process is non-Mendelian as it does not directly change the genotype. Epigenetic tags are imprinted in the germline and cause the imprinted genes to be expressed from only one parent [82].

There are three hypothesised theories for the process of imprinting

- **the kinship theory** [83] – The theory suggests that an imbalance exists between parental genes due to conflicting fitness strategies from both parents. This is mostly apparent in sexual reproduction where the father and mother have differing interests to pass on their own genes.

- **The sexual antagonism theory** [84] – This theory uses sex-specific selection pressure. It predicts an uneven allele frequency between males and females when natural selection favours one sex over the other so that offspring genes are enriched to benefit a particular sex.

- **The maternal–offspring coadaptation theory** [85] – Based on the correlation between the genes of the mother and the maternal genes of the offspring, the maternal-offspring coadaptation theory states that the offspring is more likely to inherit from its mother because it leads to a higher probability that the offspring has a positive interaction with its maternal phenotype, and the interaction leads to higher fitness.

### 6.3.2. Gene regulation

The presence of epigenetic tags enables gene regulation mechanics to occur on the tagged genes. There are multiple forms of gene regulation: gene silencing, gene activation, and gene repression. All forms of gene regulation affect the expression of the affected genes leading to variation in phenotypes from the same genotype [86]. Gene silencing is a mechanism for turning entire sections of the genotype on and off independent of mutation. In evolutionary biology gene silencing has the effect of protecting the host organism from viruses [87] by silencing genes that are used in viral reproduction. In terms of convergence and diversity, convergence should be increased and diversity decreased as silenced genes are not fully expressed compared to other genes.

Gene repression acts on individual genes rather than entire sections of the genotype. In evolutionary biology it switches off genes whose products are required to maintain cell functions [88]. To implement this computationally, each variable in a candidate solution can be switched on or off, based on the tags of the epigenotype. The modification of the tags can be based on the fitness of the individual, adapted based on the progress of the search or based on environmental cues.

### 7. Conclusion

Evolutionary Computation is an area that now covers many hundreds of different variants. Despite its biological roots, and the diversity of mechanisms available in nature, these algorithms can broadly be split into two main categories of evolution: Evolutionary Algorithms, which take inspiration from genetic inheritance, and Swarm Intelligence algorithms, which take inspiration from cultural inheritance. The reason for this lack of diversity is speculated to be that similar underlying biological mechanisms are often recycled under new banners, making it hard to understand which mechanisms have already been considered. To understand which have been considered, and which have been overlooked, existing Evolutionary Computation algorithms are categorised under a contemporary biological classification inspired by the Extended Evolutionary Synthesis. It confirms that two main types of information exchange, and therefore behaviours, are used in Evolutionary Computation. Few algorithms even go as far as combining these types of information exchange but with those that do providing excellent performance.
The framework shows that the existing concepts from the Modern Evolutionary Synthesis have already been incorporated and that some concepts of the Extended Evolutionary Synthesis have also recently been included, with benefits to performance of those algorithms. Opportunities for Evolutionary Computation with epigenetic mechanisms are identified, which is a key element of the way evolution is now described with many underlying mechanisms proposed in the biological literature. These mechanisms provide a self-adaptive means to quickly converge and stabilise populations in changing environments. A key aspect in inspiring algorithms from epigenetics is flagged as the transfer of epigenetic information to quickly change individual phenotypes, which must be reversible so that they do not alter the genotype. The resulting mechanisms will be both self-adaptive and convergence based, which could provide benefits to Evolutionary Computation.

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## Appendix A. Algorithms chosen

Table A.3: Evolutionary algorithms were chosen if they had more than 1000 citations on Google Scholar, or showed exceptional performance in a competition or benchmarking paper.

| Algorithm       | Citations | Reason                                                                 |
|-----------------|-----------|------------------------------------------------------------------------|
| NSGA-II         | 35038     | Most popular multi-objective genetic algorithm with over 1000 citations and used to represent the niching based family of multi-objective genetic algorithms. |
| MOEA/D          | 5205      | Original algorithm in the decomposition based family of multi-objective genetic algorithms. Over 1000 citations. |
| IBEA            | 1925      | An indicator based genetic algorithm using an indicator for selection, which contrasts with the common Pareto dominance ranking used for selection. Over 1000 citations. |
| HEIA            | 94        | One of the top performing multi-objective algorithm from recent benchmarking on 100 Evolutionary Computation problems representing the co-evolutionary family of genetic algorithms. |
| cMLSGA          | 6         | One of the top performing multi-objective algorithm from recent benchmarking on 100 Evolutionary Computation problems representing the multi-level selection family of genetic algorithms. |
| DE              | 25723     | Original differential evolution algorithm which many CEC single objective competition winners are based off of. Over 1000 citations. |
| SHADE           | 614       | An extension of DE with improved performance using a memorised history of successful parameters. SHADE variants have won or come top in multiple CEC competitions from 2014 to 2019. |
| CMA-ES          | 1858      | Algorithm from the family of Evolution Strategies algorithms with enhanced performance over the original ES algorithm. Over 1000 citations. |
| CLPSO           | 3253      | Popular variant of the particle swarm optimisation algorithm. Over 1000 citations. |
| ACO             | 13431     | Algorithm used primarily for path finding and routing problems. Over 1000 citations. |
| ABC             | 6625      | Algorithm based on the foraging behaviour of bees. Over 1000 citations. |
| EBO with CMAR   | 67        | Top performance in CEC'17 Bound Constrained Competition [38]. |
| FA              | 3533      | Based on the flashing behaviour of fireflies. Over 1000 citations. |
| Cuckoo Search   | 5553      | Based on the Cuckoo species laying eggs in the nests of other birds. Over 1000 citations. |
| GWO             | 5137      | Algorithm inspired by the hunting behaviour of grey wolves. Over 1000 citations. |