OVERVIEW

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From evolutionary ecosystem simulations to computational models of human behavior

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Abstract

We have a wide breadth of computational tools available today that enable a more ethical approach to the study of human cognition and behavior. We argue that the use of computer models to study evolving ecosystems provides a rich source of inspiration, as they enable the study of complex systems that change over time. Often employing a combination of genetic algorithms and agent-based models, these methods span theoretical approaches from games to complexification, nature-inspired methods from studies of self-replication to the evolution of eyes, and evolutionary ecosystems of humans, from entire economies to the effects of personalities in teamwork. The review of works provided here illustrates the power of evolutionary ecosystem simulations and how they enable new insights for researchers. They also demonstrate a novel methodology of hypothesis exploration: building a computational model that encapsulates a hypothesis of human cognition enables it to be tested under different conditions, with its predictions compared to real data to enable corroboration. Such computational models of human behavior provide us with virtual test labs in which unlimited experiments can be performed.

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KEYWORDS

agent-based modeling, cognition, evolutionary computation, evolutionary ecosystems, human behavior

1 | INTRODUCTION

In the past, a diverse range of experiments was performed on human subjects as we strove to further our understanding of human cognition and behavior. While often illuminating, such experiments sometimes used procedures that we now consider unethical (Dischereit, 2014; Zimbardo, 1973). Those times are largely over as we rightly place more emphasis on ethical and moral considerations. Computational models provide an ethical alternative that enable us to explore hypotheses of causation for specific behaviors. Instead of experimenting on real people, computational models allow us to simulate the behaviors of people in simulated environments. We can design models to investigate specific questions:

will a group of people decide to cooperate under certain circumstances? Are certain design strategies more successful when people make products to be used by others in a competitive marketplace? Will groups comprising specific personalities work together better in a team for certain tasks?

When we build such models, we typically begin with the hypothesis or question we wish to study. We define the minimum assumptions and conditions believed necessary, and run experiments to establish the validity of the hypothesis or the range of conditions for which the hypothesis is true or not. A good model focuses on the key factors that might affect the outcome of interest, and removes other potentially distracting elements.

The toolbox of available computational models is large, and as we cross disciplines, it is possible to discover new and valuable methods to further these goals. One interesting set of tools can be found in disciplines that study evolutionary ecosystems. A computational model of an ecosystem typically comprises multiple entities (named *agents*) that follow simple rules of interaction. The nature of the agents and their interactions may change over time, and indeed may be said to evolve, as some models enable selected pairs of agents to generate offspring that inherit features from their parents, with versions of genetic crossover and mutation. Models of evolutionary ecosystems may be quite abstract in nature, or they may explicitly model human groups and their behaviors. We argue that all such models may provide useful methods for the study of human cognition, and we review a selected range of classic works and exciting new approaches that have the potential to advance the way we study human behavior in the future.

2 | BACKGROUND

Evolutionary computation (EC) algorithms have been considered a natural choice for modeling ecosystems for many years, as they were inspired by natural evolution to solve problems. They use notions of genotype to phenotype mapping, where parameters that define a solution are encoded as "genes" to define a search space—a space of possible solutions to the problem. The algorithm searches this space using populations of candidate solutions, enabling a parallel search that finds solutions even to difficult problems that may have many possible solutions (Morrall, 2003; Whigham & Fogel, 2006). Evolutionary algorithms such as genetic algorithms (GAs) explicitly model evolutionary processes, often to perform optimization: evolving the best solution to a problem. For example, given a design problem, a GA will start with a population of randomly initialized solutions, and breed better candidates by enabling better solutions to have offspring, as measured by a "fitness function" which evaluates how effectively a solution solves the problem. Offspring inherit genes from their parents which are mixed in new combinations using a crossover operator and with novelty added through random mutations of the gene values. Offspring replace their parents and the algorithm evolves better and better solutions as the generations go by. By the end of the evolutionary run, the population within the GA will converge onto a good design for the problem.

When used to model ecosystems—the focus of this work—each solution may represent a living organism with its own strategy of behavior. The GA may be configured to maintain diversity (instead of the entire population converging to one solution) with the result that an evolutionary run may create a population of individuals each collaborating or competing with each other to survive. The explicit fitness function may be replaced with an implicit notion of resources—use the right strategy to gain a share of limited resources and you live, use the wrong strategy and you die, never passing your unsuccessful strategy to children. In this way, the GA starts to resemble an agent-based model that evolves over time.

In contrast to the evolutionary approaches, agent-based models (ABMs) provide a general-purpose approach to modeling complex systems with many interacting elements, such as social systems. The simple methods capture nonlinear dynamics with often easy-to-understand rules. Unlike evolutionary algorithms, a typical ABM model has no notion of evolution—usually, the model starts with a specific set of agents with specific behaviors, and no new agents are created or lost. In these algorithms, agents behave as autonomous entities with their own individual memories, sensors, and actions. Agents might interact with their environment (e.g., consuming resources or leaving a scent trail) or they might interact with each other (e.g., communicating to cooperate, or to compete). The interaction between agents can often lead to emergent behavior useful in modeling complex systems—just because the rules of interaction between agents are simple, does not mean the resulting behavior of the agents will be predictable.

ABMs are widely used in research areas including sociology, biology, cognitive science epidemiology, and ecology (Bentley, 2009; Cuthbert et al., 2017; Farmer & Foley, 2009). Sometimes the space of possible ABM parameter settings is explored or optimized by genetic algorithms or other techniques, merging these two approaches once again.

Evolutionary ecosystems are thus typically some mixture of EC and ABM, some researchers using more of the tools of one than the other, some using a more even balance. These techniques are merged to form a distinct kind of research, one that follows a clear methodology. We can summarize the features of such work performed at the intersection of EC and ABM as the following:

- Hypothesis-based modeling;
- Emphasis on modeling individual entities and their interactions with each other and their environment;
- Emergent results arising from complex interactions that may not be predictable in advance;
- Widely used, tried, and tested approaches for a variety of disciplines; and
- Good availability of resources from example code to analysis techniques.

While these features may not be unique to this combination of EC and ABM, the methodology of evolutionary ecosystems approaches is centered around such characteristics, and we argue that this is highly beneficial for researchers wishing to study human behavior. Having defined the fundamental computational approaches, we explore three relevant types of existing research on the simulation of evolutionary ecosystems, transitioning from more abstract and general models to models aimed specifically at understanding human behavior: theoretical ecosystems, nature-inspired evolutionary ecosystems, and evolutionary ecosystems of humans. The following sections describe work in these areas; we end with a look at the current efforts at using combinations of EC and ABM for cognitive science.

2.1 | Theoretical ecosystems

It is common for researchers to use abstract and theoretical models that do not model one system explicitly but may be used to elucidate a class of systems. The use of the Iterated Prisoner's Dilemma (IPD) is common: the game where two prisoners decide whether to cooperate or defect, are rewarded most if they defect and the other cooperates, and are penalized most if both defect. When played repeatedly (for a number of repetitions that is unknown to the players), the best strategy for a given payoff matrix depends entirely on the strategy of the other player and may change over time. One of the first examples of using the IPD in combination with genetic algorithms was Axelrod's classic work (Axelrod & Hamilton, 1981) which demonstrated how different stable strategies of cooperation could evolve over time (Figure 1).

Many researchers have followed in his footsteps, for example, Ishibuchi and Namikawa (2005) formulated a spatial Iterated Prisoner's Dilemma (IPD) game that introduces "structured demes." They use a twin "neighborhood structure" with one deme determining the interaction according to the IPD game, and the other used to determine who mates with whom. The separation models the idea that some interactions are transitory and spatially distant, for example, a tourist visiting a shop for souvenirs may never return, but he/she may develop a generic strategy for how to participate in interactions with souvenir shops. Their investigation discovered how the size of the interaction neighborhood and the probability of mistakes in implementing strategies affected the evolution of cooperation, concluding that "the use of a small interaction neighborhood facilitated the evolution of cooperative behavior even in the situation with a relatively high mistake probability." In a similar vein, Chong and Yao (2007) conducted a series of investigations to understand reputation. To add a little more realism, they modified the original IPD to enable more choices (different levels of cooperation or defection) and concluded that, "when there are more choices, strategies have more opportunities to exploit others by playing lower cooperation levels." However, with the introduction of reputation, the likelihood of cooperative behavior was increased. Further examples of studies (out of many hundreds) in theoretical ecosystems can be found in Table 1, focusing on research relating to evolutionary ecosystems.

2.2 | Nature-inspired evolutionary ecosystems

Some researchers are inspired more directly by ecosystems in nature. Although their models may also be simplified compared to reality, they often incorporate some notion of resources that agents compete to obtain.

Daisyworld by Watson and Lovelock (1983) was one of the earliest ecosystem models and provides a simple example of an evolutionary ecosystem. It comprises an imaginary planet with a simple biosphere that consists of daisies colored black or white. The growth rate of the daisies depends only on temperature, with white daisies better able to survive in
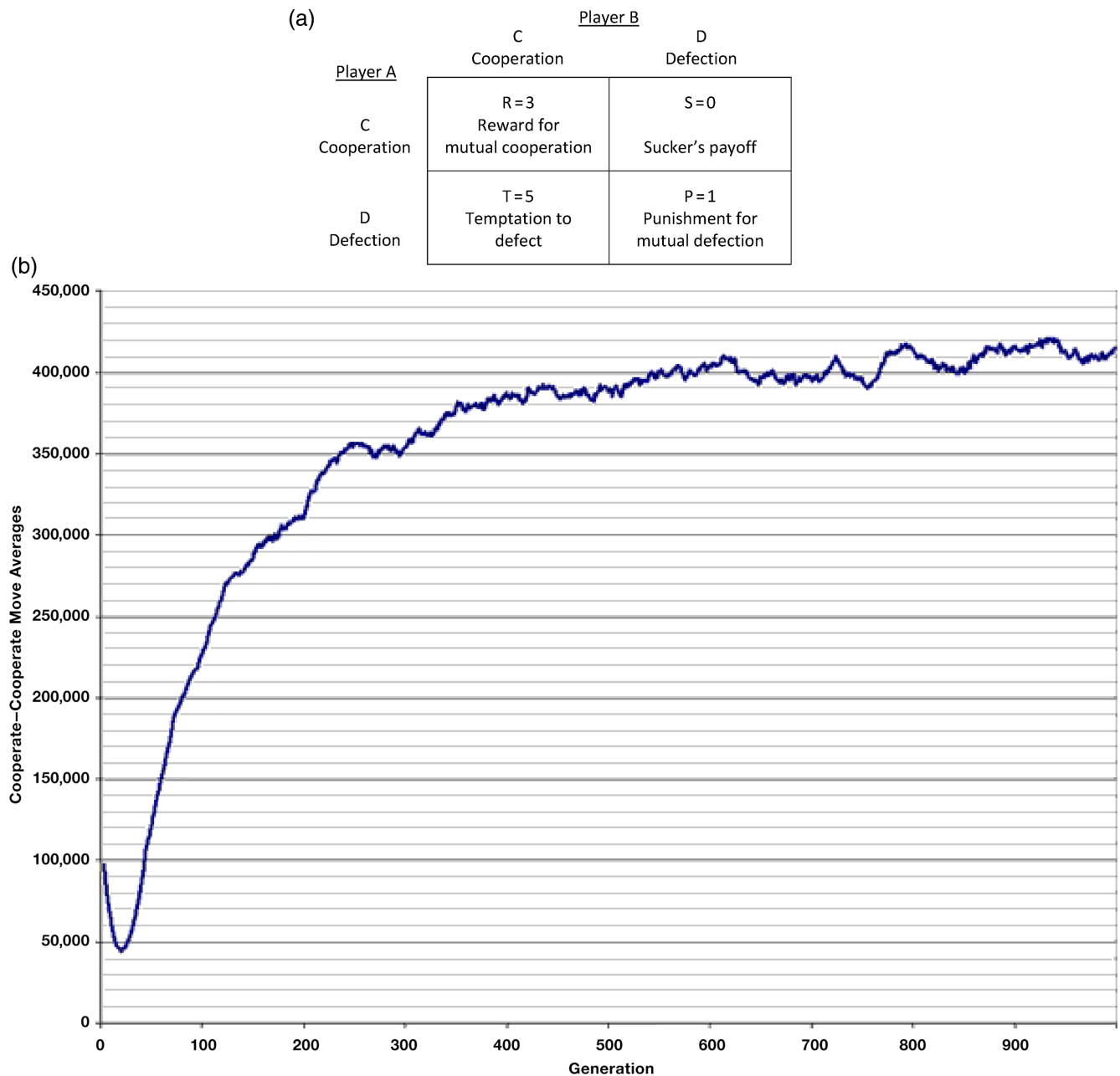
(a)

	Player B	
	C Cooperation	D Defection
Player A		
C Cooperation	R = 3 Reward for mutual cooperation	S = 0 Sucker's payoff
D Defection	T = 5 Temptation to defect	P = 1 Punishment for mutual defection

(b)

FIGURE 1 (a) The Prisoner's dilemma game. A typical payoff matrix is shown for Player A; values should satisfy the relationship T > R > P > S and R > (S + T)/2. From Axelrod and Hamilton (1981). (b) Cooperate–cooperate move averages, by generation, for 100 trials. From Hourigan and Eck (2004)

warmer conditions and black better able to survive in cooler conditions, while numerous white daisies cause a cooling effect and numerous black daisies cause a warming effect to the planet (Figure 2). Analysis showed a remarkably robust behavior, unaffected even by major alterations of environmental feedback: the two populations of daisies evolve to stabilize the temperature in the world.

More recently, Echo was created as a platform to study ecosystems in general. Agents evolve in an environment with limited resources (Holland, 1992; Hraber et al., 1997). Agents may interact through mating, trade or combat, and evolve survival strategies to use the appropriate form of interaction at the right time, resulting in resource regulation across the environment. Echo was compared with systems of biology using analysis comprising species-area scaling relation and the Preston distribution (Hraber et al., 1997).

Ward et al. (2001) developed a model where agents ("artificial creatures") live in a simulated environment with hazards and resources for food. They evolve behaviors intended to resemble schooling, using "neural network brains"

TABLE 1 Theoretical ecosystems

| Name/focus	Description	Results/findings	References
Monomorphic evolutionarily stable ecological equilibrium	A combination of two models: evolutionary game theory and Lotka–Volterra model of population ecology, which assumes all individuals in each species behave identically.	Introduction of the evolutionary ecology stability concept, with Maynard Smith's original definition of an evolutionarily stable strategy for a single species as a special case.	(Cressman & Garay, 2003)
Complex interactions with incomplete information	A theoretical analysis of the interactions of partially cooperative agents in situations with incomplete information, focusing on the case of two types of agents, each with two strategies.	Agents can find suitable strategies through evolution and adaptation and for two or more strategies can find a steady state.	(Sim & Wang, 2005)
Scenario calculus	Introduces a new method for analyzing features of complex systems with emergent behaviors, looking at convergence, and other agent parameters.	The experiments uncovered dynamic features relating to convergence that were very difficult to obtain by formal logic.	(Wang & Zhu, 2007)
Complex coevolutionary dynamics	An investigation of how theoretical analyses of infinite-sized coevolving populations may not apply to more realistic finite-sized populations.	Infinite population simulations do not always represent real trajectories and are not always representative of co-evolutionary dynamics of large and finite populations.	(Tino et al., 2013)
Coevolution and games	Explores cycling behaviors in the context of coevolving game-playing individuals, using the game Othello.	The method was able to find strong value functions in an experiment evolving weighted piece counter value functions to play the Othello board game.	(Samothrakis et al., 2013)
ABM parameter search with complexification	Studies complexification approaches with evolution to aid evolution in finding parameter values for agent-based Boid and Bee models automatically.	Both models benefited from the use of complexification, which improves evolutionary algorithms when the use of genomes with variable length and complexity is possible.	(Wagner et al., 2015)
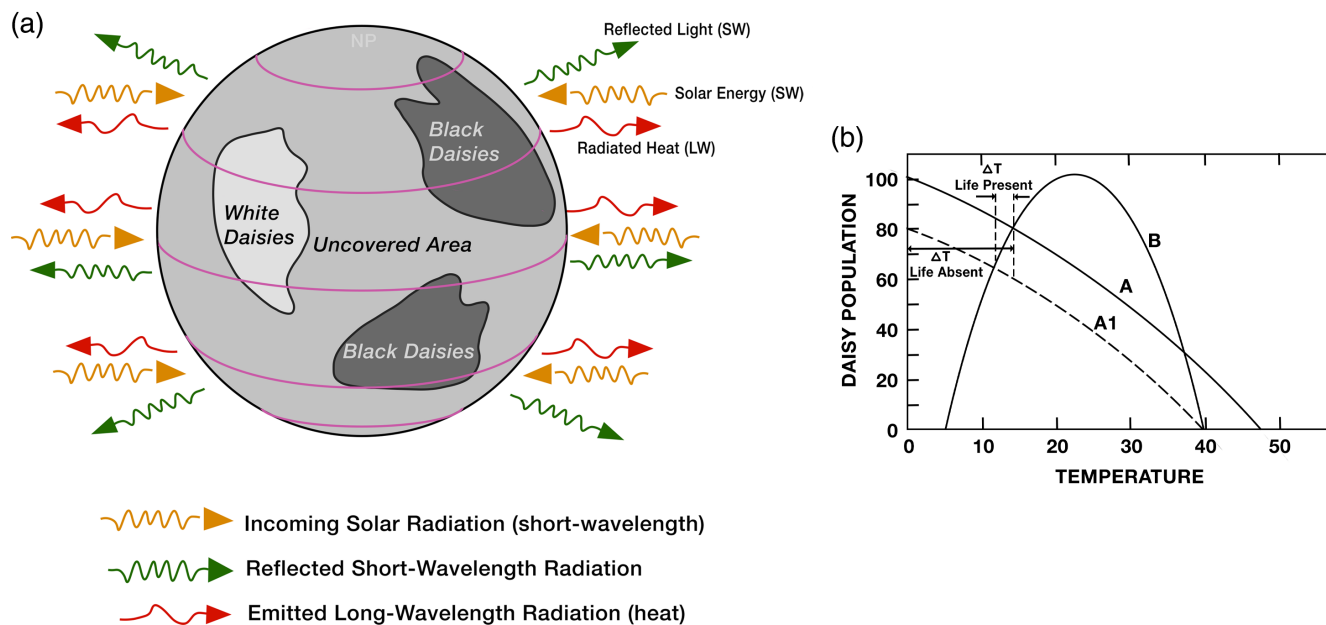
FIGURE 2 (a) Schematic model of Daisyworld, whose surface is covered by black and white daisies and empty area. The temperature of Daisyworld is related to how much energy is received and how much is reflected; the difference is the amount of solar energy absorbed. The amount of energy reflected back to space depends on the planet's albedo (the fraction of light energy that is reflected). The albedo in turn depends on the coverage of white and black daisies. The heat radiated to space is a function of how much energy is absorbed. (b) Line A shows daisy cover against Daisyworld temperature, plotted here for white daisies. More of these daisies will reflect more radiation and so the mean temperature will be reduced. Line B shows the growth of these daisies at different temperatures. Line A1 illustrates less incoming solar radiation on the daisies, showing that the world will cool by 16 degrees unless the daisies respond. If the daisies respond by dying back, the difference dTl in world temperature is only 2 degrees. According to Lovelock (1986), "This simple responsive coupling between life and its environment is the basis of geophysiological regulation."

specified by chromosomes, allowing details of the network to be inherited by offspring. They model predators and prey and observed the spontaneous development of complex schooling behavior without explicitly defining values for schooling in the fitness function.

Alfonseca and Gil (2015) described another predator–prey ecosystem. Their agents ("artificial beings") were comprised of mathematical fitness functions that evolved using grammatical evolution to form different niches in a non-spatial environment with limited resources. The diversity and rate of change of the evolution were analyzed over time, showing that the artificial ecosystem displays many properties of biological ecosystems, despite being constructed from entirely abstract mathematical beings. They attempted to draw conclusions from their models about how natural evolution may progress, stating that "some of the features displayed by biological evolution may depend to some extent on chance modifications of the genome plus natural selection, rather than on the particular form adopted by the phenotypes."

There is a plethora of other nature-inspired ecosystems with evolutionary dynamics within interacting populations. For brevity, further examples are summarized in Table 2 ordered chronologically by date of publication, focusing on well-known, and recognized systems.

2.3 | Evolutionary ecosystems of humans

While previous work explored more abstract models, often relating to nonhuman systems, simulation or agent-based modeling is being used increasingly to investigate social and economic issues in human societies and groups (Gilbert & Troitzsch, 2005). Many of the simulations are evolutionary.

Dawid et al. (2001) studied firms in their agent-based model, with each agent representing an entire company. For every discretized time step, a firm interacts according to several options: it may duplicate the product of a rival, create a new variation of a product, or continue to produce existing products. Each firm may have different capabilities to

TABLE 2 Nature-inspired evolutionary ecosystems

Name/focus	Description	Results/findings	References
Bugs world	A two-dimensional lattice with adaptive bugs and food whose distribution changes over time by diffusion.	Early example of intrinsic adaptation is where evolution is driven by many interacting subsystems, without an explicit fitness function.	(Packard, 1989)
Tierra	An ecosystem of evolving computer programs that are competing for processing time and memory space.	An exploration of fundamental processes of evolutionary and ecological dynamics such as punctuated equilibrium, host–parasite co-evolution, and density-dependent natural selection.	(Ray, 1991)
Evolutionary reinforcement learning (ERL)	A model where adaptive agents travel across a two-dimensional lattice at random, encountering food, predators, hiding places, and other items.	Learning and evolution together are more successful in producing adaptive populations compared to either alone.	(Ackley & Littman, 1991)
Avida	A Tierra-inspired (Ray, 1991) evolutionary biology software platform to conduct experiments with self-replicating and evolving computer programs.	Spatial geometry helps the development of diversity and adaptive capabilities.	(Adami & Brown, 1994)
PARE	Parasitoid Artificial Ecosystem, a parasitoid/host model based on parasitic wasps and their insect hosts in natural systems.	Large population sizes can be achieved in artificial models where the dynamics mimic natural systems and are derived through the behaviors of independent components.	(Olson & Sequeira, 1995)
Swarm	An agent-based simulation of a collection of agents performing a string of actions.	Swarm supports hierarchical modeling approaches.	(Minar et al., 1996)
Sugarscape	One of the earliest artificial worlds consists of agents, rules, environment, and sugar, the only food source for agent survival.	Has been used to investigate social dynamics including marital status, inheritance, and evolution.	(Epstein & Axtell, 1996)
PlantWorld	A 2D grid world upon which stationary agents, i.e., plants, germinate from seeds, maintain themselves, grow, reproduce, and die.	A demonstration of feedback between population attributes and evolutionary dynamics dependent on environmental perturbations.	(Dyer & Bentley, 2002)
Evolve IV	An evolutionary ecosystem model that is individual-based and metabolically driven.	The model captures the reciprocal interaction between biota and their surroundings, for example, the initial population pollutes the environment to its own detriment.	(Brewster et al., 2002)
Organism Interaction	An artificial life model where organisms fight for space and resources but can also form mutualistic relationships.	When organisms gather a certain amount of nutrition, reproduction and mutation occur, and mutation creates new varieties of organisms.	(Pachepsky et al., 2002)
Mosaic World	An evolutionary ecosystem where "critters" evolve visual receptors and behaviors in a visually ambiguous world.	Explores computational principles by which color vision can emerge, overcoming ambiguity and usefully guiding behavior.	(Schlessinger et al., 2005)

(Continues)

TABLE 2 (Continued)

Name/focus	Description	Results/findings	References
Masbiole	A multi-agent simulation that uses symbiotic learning and evolution where agents can learn or evolve depending on their symbiotic relations toward other agents.	Masbiole agents can escape Nash equilibria and can be used to solve general computational problems such as optimization.	(Eguchi et al., 2006)
Singing robots	A group of autonomous robots that interact and imitate each other using vocal-like sounds to create music.	The robots learn to imitate each other by babbling heard intonation patterns to evolve vectors of motor control parameters to synthesize the imitations.	(Miranda, 2008)
EcoSim	An individual-based predator–prey model where each agent behavior is characterized by a fuzzy cognitive map, allowing the agent's behavior to evolve as the simulation runs.	The simulation shows coherent behaviors with the emergence of strong correlation patterns also observed in existing ecosystems.	(Gras et al., 2009)
EcoDemics	A model of epidemic spread in EcoSim (Gras et al., 2009).	The dynamics of the ecosystem, along with the spatial distribution of agents, play a significant role in disease progression.	(Majdabadi Farahani, 2014)
Evolutionary geometric agent-based model	Incorporating evolutionary algorithms in Geometric Framework combined with agent-based models to explore nutritional strategies of agents in the presence of competition.	Competition combined with reproductive skew in social groups can play a role in the evolution of diet breadth.	(Senior et al., 2015)

T A B L E 3 Financial markets

Name/focus	Description	Results/findings	References
Santa Fe artificial stock market	An artificial stock market in which independent adaptive agents can purchase and sell stock.	The market behavior is an emergent outcome of the agent's behavior, and it can include bubbles and crashes.	(Palmer et al., 1994)
Trade Network Game (TNG) Laboratory	A computational model for studying the emergence of trade networks among sellers, dealers, and buyers.	Agents look for trade partners, participate in risky trades, which are modeled as noncooperative games, and evolve their strategies over time.	(McFadzean et al., 2001)
Foreign exchange	An artificial model of a foreign exchange market is developed using a genetic algorithm, with agents having internal representations of market situations.	A quantitative explanation of micro–macro relations in markets corroborated with real-world data. Emergent effects were explained by a "phase transition of forecast variety," caused by the interaction of demand–supply and agent forecasts.	(Izumi & Ueda, 2001)
Macrofinance	An agent-based simulation of the stock market where participants adapt and evolve as the simulation runs.	Agents coevolve their trading rules based on different levels of past data while trying to optimize their wealth.	(LeBaron, 2001)
Investment trading	An artificial financial market was developed to study stock markets. The model consists of three types of traders: noise traders, fundamental traders, and technical traders, each with a different trading strategy.	The work showed that evolutionary computation can be used to study stock markets and identified which conditions were necessary to produce realistic behaviors.	(Martinez-Jaramillo & Tsang, 2009)
Bounded rationality of trading	An artificial market model with selection pressures to study whether bounded rationality observed in trade behaviors could have an evolutionary basis.	A decision-making model with bounded rationality has the capacity to become a stable evolutionary strategy and entities with bounded rationality can survive in a competitive market.	(Kinoshita et al., 2013)

innovate or imitate; all firms have the ability to estimate the potential of markets. The authors investigated how the novelty of products correlates to profitability, looking at firms individually, and as an entire industry.

Evolutionary models that seek to understand human behavior with respect to organizations and finance are common. Table 3 provides examples of existing evolutionary financial markets, Table 4 provides examples of other man-made markets, and Table 5 provides examples of organizational behavior, all examples chosen based on relevance to this topic. For more examples and models also refer to Tesfatsion (2002) and Tesfatsion (2015).

Moving directly into the domain of Cognitive Science, models of human systems have been used to explore strategies employed by individuals for a diversity of tasks. Mesoudi (2008) simulated the evolution of culture using the notion of arrowhead design. Their agents ("participants") created "virtual arrowheads" which were assessed in "virtual hunting" environments. Like the modeling of firms above, the designs could be modified by imitating the design of rivals, or through incremental improvement. Their results demonstrated the value of imitation—"copy-successful-individuals" was the winning strategy. Beuls and Steels (2013) also explored cultural evolution, examining the evolution of human language over time. Their model uses agents defined as "speakers" and "hearers" that pass language elements to each other and model the emergence of agreement between them. They concluded that "agreement systems thus help to minimize cognitive effort and maximize communicative success," while also making the point that their models were "a powerful illustration of agent-based modeling, which is a novel way of studying the origins of grammar."

Modern technologies also influence our behavior, and some models explore these new dynamics in our societies. For example, Nikolic and Dijkema (2010) developed a modeling process based on evolutionary computation, which optimized agent-based models of "large scale sociotechnical systems" including energy, water, and transport infrastructures. Another example is the creation of software products that are then sold via online marketplaces, such as App Stores. AppEco, developed by Lim and Bentley, is an agent-based model of the iOS Apple Store and was used to study app developer strategies (Lim & Bentley, 2012b), effects of publicity on app download (Lim & Bentley, 2012a), and the

TABLE 4 Other markets

Name/focus	Description	Results/findings	References
Labor market	A model of the labor market where agents use energy to find jobs by direct job search or making friends who would tell them about jobs. Agents who run out of energy will die and agents who gain sufficient energy will reproduce by cloning another agent who has similar social networks and search strategies.	The model discovers individual robustness for surviving job losses can result in overall loss in population efficiency, with implications for new policies that could be implemented.	(Tassier & Menczer, 2001)
Electricity trading	An evolutionary model of a detailed, plant-by-plant simulation of the new electricity trading arrangements (NETA) in the UK where agents learn and modify their actions with the purpose of maximizing their own profit.	The model was able to make predictions for pricing and strategic insights relevant to NETA.	(Bunn & Oliveira, 2001)
Wholesale electricity market	An agent-based model of a wholesale electricity market where electricity pricing is determined by a clearinghouse double auction, where buyers and sellers participate repeatedly in auction rounds.	High market efficiency is achieved and market microstructure is predictive of the relative market powers of buyers and sellers.	(Nicolaisen et al., 2001)
Fish market	A model of a wholesale fish market where sellers decide on supply quantity, asking price, and how to treat loyal customers, using evolutionary algorithms such as genetic algorithm, hill climbing, and annealing schedules, and buyers decide on who to buy from and the prices they would accept.	The model explains both stylized facts price dispersion and high loyalty, it also explains the effect of heterogeneity of the buyers.	(Kirman & Vriend, 2001)
Labor productivity	An evolutionary agent-based model of output- and labor-market dynamics where firms, using labor as the sole input under a constant returns to scale regime, produce a homogeneous, perishable good. Labor productivities are specific to each firm and alter stochastically as a result of technical progress. The model allows for a process in which firms are chosen based on their demonstrated competitiveness.	The model generates predictions about how system parameters affect aggregate performance and its volatility.	(Fagiolo et al., 2004)
Consumer market	An artificial world was developed to investigate the effects of organizational learning strategies on consumer market share.	The simulation demonstrated that different learning strategies work better depending on the environment and timing.	(Lu et al., 2008)

effect of app store ranking algorithms on downloads (Lim & Bentley, 2013). They also modeled the evolution of app developer strategies in the app store to understand the relationship between stability and fitness (Lim et al., 2015). The AppEco model can be found in Figure 3.

Such models can even be used to study psychological theories of human behavior. For example, the personality of individuals in a team plays a key role in whether the team will be successful or not (Barrick et al., 1998;

TABLE 5 Organizational behavior

Name/focus	Description	Result/findings	References
Organizational governance	An agent-based model of an economic society where agents have their own goals and protect their self-interests. They can also change their behaviors in response to interaction with other agents and the environment.	Goals at the macro level can be achieved without controlling self-interested economic agents at the micro level.	(Takadama et al., 2001)
Human resource management	An evolutionary computational model to study the migration decisions of individuals in an organization, which is influenced by their own characteristics and that of the environment, such as organizational culture.	Artificial worlds enable experiments relating to people that are infeasible to perform in the real world.	(Chen et al., 2002)
Civil violence	A model to study civil violence using the spatial evolutionary multi-agent social network in which agents evolve their strategies over time using independent learning and collective coevolution.	The simulation shows the emergence of interesting patterns in group movement and behavioral development.	(Quek et al., 2009)
Consensus	A model to explore the evolution of consensus, where a population of simulated organisms subject to mutations and natural selection, is placed into groups whose fitness depends on their ability to reach consensus in a user-defined environment.	Genetic heterogeneity within groups increases the difficulty of the consensus task, but groups were able to overcome these obstacles and evolve this cooperative behavior.	(Knoester et al., 2013)

Bell, 2007). Human personality is often divided into five basic, universal dimensions of individual variation known collectively as the Big-Five, namely (i) neuroticism—a tendency to experience negative emotions such as anxiety and anger, (ii) extraversion—an inclination to be gregarious, assertive, and active, (iii) openness to experience—the propensity to be intellectually curious and prefer variety, (iv) agreeableness—a predisposition towards working collaboratively, and building social harmony, and (v) conscientiousness—the propensity for orderliness and self-discipline (Costa & MacCrae, 1992; Goldberg, 1990). This is in contrast to Jung's type theory which classifies human behavior by two perceiving functions (sensing and intuition) and two judging functions (thinking and feeling), which are modified by two attitude types (extraversion and introversion) (Jung, 1923).

Researchers in agent-based modeling has begun using personality to determine agent behaviors. Early models offer interpretations that loosely match literature in psychology, are context-dependent, and largely unverified (Ahrndt et al., 2015; Salvit & Sklar, 2012). More recently, Lim and Bentley (2018) created a model to study how teamwork could be affected by personality. The general-purpose model used a novel combination of techniques: the changing "direction of thought" over time was modeled by a customized swarming algorithm, originally developed to model the way birds flock. Each agent changed its ideas and was influenced by other agents according to its unique personality traits, modeled on Jung's type theory (Lim & Bentley, 2018). A team of such agents would then be set a task—to solve some problem together. Genetic algorithms (GAs) were used to explore which combination of traits could improve or worsen group performance. The model was used to examine the effects of team diversity in individual backgrounds (Lim & Bentley, 2019a), the effects of dynamic problems (Lim & Bentley, 2019b), and the effects of reward sensitivity (Guo et al., 2020). They also created a new model using the Big-Five trait theory as the personality model (Lim et al., 2022). This study used a GA to explore the limits of the ABM to discover which combination of traits correlated with the best and worst performing teams for a problem with different levels of uncertainty (noise). The model predicted that higher average team agreeableness correlated with better performance for tasks with uncertainty. The prediction was confirmed with data gathered over more than a decade comprising 3698 individuals in 593 teams on tasks with and without uncertainty.
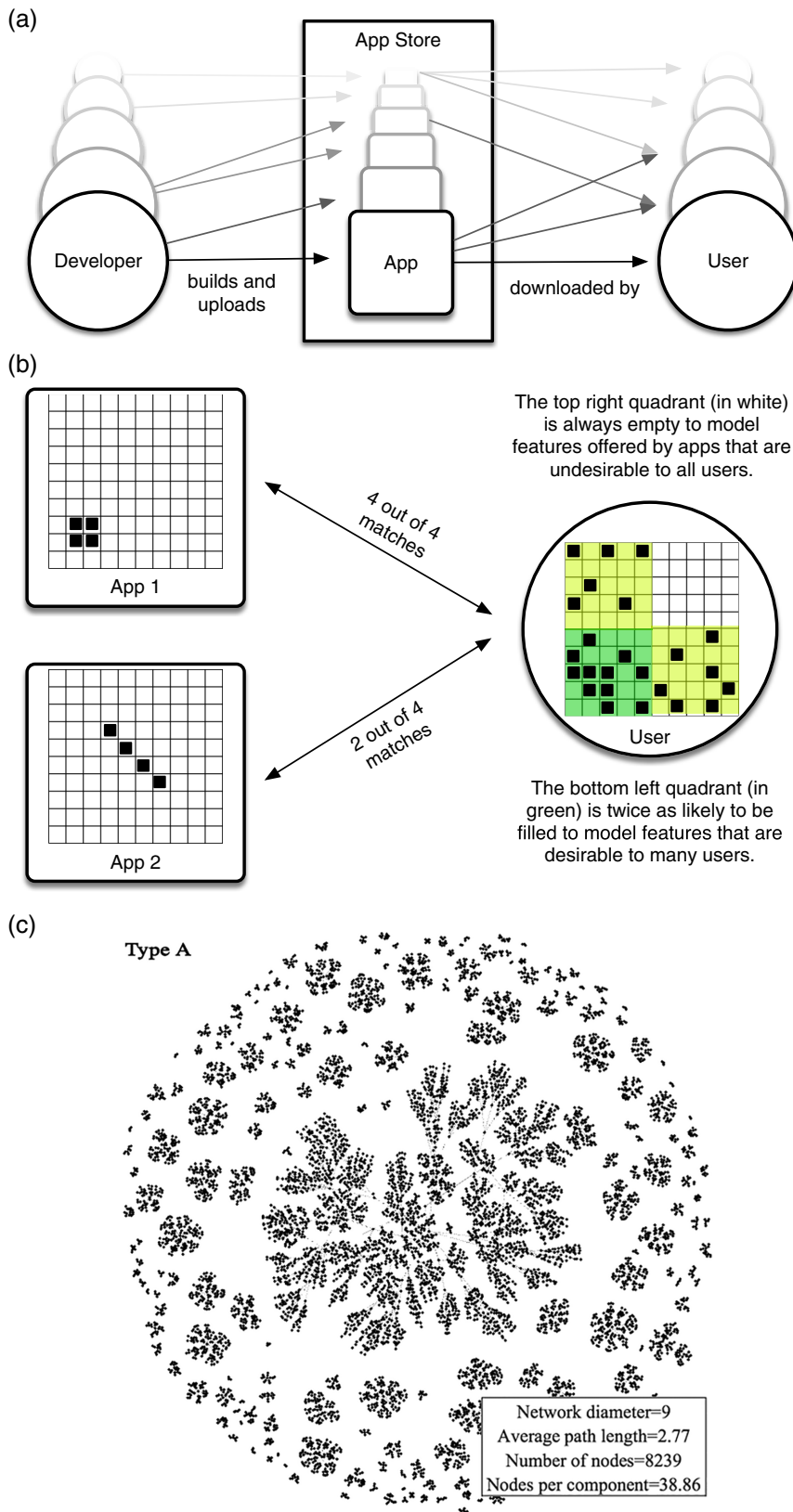
FIGURE 3 (a) Overview of AppEco showing how developers build apps, which are listed in the App Store and downloaded by Users. (b) Matching user preferences with app features. (c) A view of app spread through a network of users after a "Mass Exposure" media event. From Lim and Bentley (2012a) and Lim et al. (2015)

TABLE 6 Cognitive science and psychology

Name/focus	Description	Results/findings	References
Iterated learning model (ILM) for language	A computational model of the transmission of linguistic behavior over time that does not explicitly implement natural selection.	Evolution of language was observed driven only by "general pressures" of language transmission.	(Kirby, 2001)
Language evolution	A framework for studying iterated learning with rational Bayesian agents.	Suggests a formal connection between how language can be acquired and the structure of languages spoken.	(Griffiths & Kalish, 2007)
Marriage and divorce annealing model (MADAM)	An ABM is based on homophilic trait matching in which individuals search for mates similar to themselves but relax these expectations as they age.	Increasing population heterogeneity and reducing the rate of relaxing expectations can both increase the average age of the first marriage.	(Hills & Todd, 2008)
Social identity dynamics	An agent-based model in which agents adopt a social group based on an optimal group size preference.	The assumptions of optimal distinctiveness theory do not lead to individually satisfactory outcomes when all individuals share the same social environment. The effectiveness of a social identity decision strategy depends on the sociospatial structure.	(Smaldino et al., 2012)
Memory transmission	An ABM is grounded in psychological theory to investigate the transmission of information within large groups.	Agents are influenced not only by neighbors but also by more distant agents, suggesting a link between the transmission of behavior and information.	(Luhmann & Rajaram, 2015)
Origins of language learning	A comparison between two models of language learning: linguistic nativism versus social learning.	Authors claim that based on their experiments the strong nativism hypothesis for language is false.	(Thompson et al., 2016)
Cultural group selection	An ABM was developed in which "cooperative" cultural traits were only selected due to the beneficial effects.	Authors suggest that hypothesis-based ABMs offer a useful source of alternative theories for cultural group selection.	(Singh et al., 2016)
Multi-person conversation	An ABM to study multi-person conversation.	Explanation of why members of minority or marginalized groups talk less; this is more pronounced in larger groups; despite talking less, they are perceived to talk more; they are more likely to be interrupted.	(Marghetis et al., 2018)
Social approach to rule dynamics	An ABM to understand the rules and exceptions function from a sociolinguistic perspective.	New learners play an important role in shaping the dynamics of rule systems in language, and large-scale social shifts in a population such as growth and turnover play an important role.	(Cuskley et al., 2018)
Incentives for priority of discovery	An evolutionary agent-based model of a competitive scientific process.	Rewarding the priority of discovery causes populations to culturally evolve towards lower quality research. Reforms such as registered reports or pre-registration may result in improved research quality.	(Tiokhin et al., 2021)

Such work demonstrates that combining evolutionary computation with ABMs in this way provides a novel methodology for the scientific investigation of human cognition, making new predictions, and improving our understanding of human behaviors. The models need not be abstract or totally removed from reality—they may be closely modeled on real phenomena with behaviors validated using real data, and their novel predictions can be verified by analysis of actual data (Lim et al., 2022).

2.4 | Psychology and cognitive science

The challenge in using evolutionary ecosystems in cognitive science is knowing how to adapt them so they are relevant to important questions in the understanding of cognition. To date, researchers have yet to discover the benefits of this combination of evolutionary computation and agent-based modeling and typically use at most one rather than both elements. For example, Smith and Conrey (2007) suggested agent-based modeling as a new approach for building theory in social psychology, citing Schelling's model (Schelling, 1971) as a social psychological example of social segregation and Axelrod's model of the evolution of cooperation (Axelrod and Hamilton, 1981). They highlighted potential obstacles to its adoption in the field, including lack of modeling training, difficulty in identifying the correct balance between simplicity and complexity, and resistance to expressing human behavior in computer code (Smith & Conrey, 2007). A few years later, Hughes et al. (2012) suggested that ABM has good potential to be used in organizational psychology.

Recently, Madsen et al. (2019) suggested using ABMs in cognitive science, pointing out that computational cognitive models that are traditionally used in cognitive science are "closed-form" or "analytical" models which describe individual behaviors in isolation and face limitations when used to predict complex human behaviors. Cognitive functions unfolding in complex systems cannot be solved analytically. The researchers suggested that ABMs can be used to calibrate and validate or test cognitive models, run controlled and repeatable simulated experiments of key variables, test longitudinal models, and run experiments that would be unethical if conducted on real people, and ABMs can provide a methodological framework to span the gap between individual-level cognitive models and population-level sociological questions (Madsen et al., 2019).

Other researchers share the same views: Kashima et al. (2017) reviewed the application of ABM to the study of cultural dynamics. They show their openness to evolutionary agent-based models by summarizing research including the evolution of cooperation work from researchers such as Axelrod and Hamilton (1981) and Nowak (2006). Yet despite many researchers focusing on topics such as learning, culture, and language where evolution may play a fundamental role, the incorporation of methods from evolutionary ecosystems (or evolutionary computation) is less common, as exemplified by the relevant studies provided in Table 6 where only the last paper uses EC with ABM, while the others are pure ABM. In the wider literature, the ideas of evolutionary ecosystem models often remain disconnected from cognitive science. The advantages of exploiting methods from evolutionary ecosystem modeling are clear, as can be seen from the examples in this article: the emphasis on hypothesis-based modeling of individual entities and their interactions with each other and their environment enables models to be constructed with a clearer methodology and accurate representation of the phenomenon being modeled. The fact that emergent results arising from complex interactions are frequently observed means there are many examples of analysis and testing available. Evolutionary ecosystems have been developed for decades so there is no shortage of examples and code to work from when creating new models. We have a long history of creating successful models of evolutionary ecosystems—these successes should be used to enhance future models in cognitive science, perhaps through collaboration, and greater interdisciplinary work.

3 | CONCLUSION

Science progresses best when findings and techniques from different disciplines are combined. Cognitive Science has a rich history of doing exactly this. We argue in this work that by focusing specifically on the techniques and methodology used within evolutionary ecosystem modeling we can learn from the diversity of agent-based and evolutionary approaches, and make use of new data-rich analyses of the complex dynamics of human and natural systems. Today our computational resources are sufficient that we are less limited by scale or complexity. We can create models comprising millions or billions of agents, each with its own unique behaviors. We can explore dynamic behaviors that depend on the actions or state of mind of others, and we can explore how behaviors might evolve over time, changing entire populations. We can perform virtual experiments, generating as much data as we like. Such data can be analyzed in detail and compared with real-world data, enabling us to explore the validity of different theories of human cognition and determine new correlates or factors that may impact their predictive accuracy.

AUTHOR CONTRIBUTIONS
Peter Bentley: Conceptualization (equal); resources (equal); writing – original draft (equal); writing – review and editing (equal). **Soo Ling Lim:** Conceptualization (equal); resources (equal); writing – original draft (equal); writing – review and editing (equal).

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The authors have declared no conflicts of interest for this article.

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Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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