Emerging diversity in a population of evolving intransitive dice

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Exploiting the mathematical curiosity of intransitive dice, we present a simple theoretical model for coevolution that captures scales ranging from the genome of the individual to the system-wide emergence of species diversity. We study a set of evolving agents that interact competitively in a closed system, in which both the dynamics of mutations and competitive advantage emerge directly from interpreting a genome as the sides of a die. The model demonstrates sympatric speciation where new species evolve from existing ones while in contact with the entire ecosystem. Allowing free mutations both in the genomes and the mutation rates, we find, in contrast to hierarchical models of fitness, the emergence of a metastable state of finite mutation rate and diversity.

I. INTRODUCTION

Evolution is the optimization scheme of the biological realm: with the correct initial conditions and ample time, random mutations and natural selection are sufficient to ensure the emergence of highly complex organisms. But the nature of what is being optimized is context-dependent. Even for a fixed environment, evolution does not necessarily have a single goal. If we were to rerun the "experiment" of evolution, it is virtually guaranteed this would result in species distinct from those that are alive today.

Evolution of specific biological features of a species depend on properties of the other species in its environment [1,2]. Such *coevolution* is believed to be central to describe evolution on the large scale [3–7] as implied by the *Red Queen hypothesis* of Van Valen [8,9]. Further, species interactions are not necessarily ranked, as observed among corals, plants and microbes [10–14]. Many studies have been devoted to understanding and evolving such intransitive interactions, ranging from molecular scale autocatalytic network [15–17] to extensions of the competitive game of rock, paper and scissors [14,18–27].

Nonhierarchical species dynamics can readily be studied for a set of species whose interactions are fixed. Here, in contrast, we are interested in evolving systems where intransitive interactions emerge *ex nihilo*. We suggest a minimal model for such a system consisting of individuals that interact by rolling dice.

II. MODEL

We define the characteristics of an individual in our system by its genome as given by a list of n integers. We only consider competitive interactions between species and settle these by interpreting the genome of integers as the sides of dice that are rolled. The outcome of a fight is stochastic, but certain dice will tend to out-compete other dice. For instance, a fight between $A = (3, 3, 3, 3, 3, 6)$ and $B = (2, 2, 2, 5, 5, 5)$ will

typically be won by A despite $\sum_i A_i = \sum_i B_i$. The probability of A winning in the present example is $n^{-2} \sum_i \sum_j [A_i > B_j] = 7/12$. What makes this particular interaction interesting in the context of competing species is the fact that we can introduce a species C such that both $B \succ C$ and $C \succ A$, or succinctly: $A \succ B \succ C \succ A$. This is for instance the case for $C = (1, 4, 4, 4, 4, 4)$. See Fig. 1 for a more complicating of five nine-sided dice interacting intransitively. This intransitive behavior of dice is well-known [28,29], but its applicability and simplicity for modeling coevolution are unexplored.

A plethora of systems could be designed around the above interaction rule. We choose to consider one of the simplest and study k individuals that interact in a well-mixed scenario. At each time step of our simulation, we let each individual randomly attack another. Two individuals, X and Y, are considered to belong to the same species if $\sum_i |X_i - Y_i| < \delta$, in which case they will not fight. Otherwise, the losing individual of the competition will be replaced by a copy of the winner. On ties, a random winner is chosen.

A crucial novelty of our model is that the dice interpretation not only sets the rules for interactions but also naturally provides a genome space in which mutations may occur. In our model, at each time step, each individual mutates with probability μ. A mutation event is the random change (± 1) of one of its genome digits. As dice that are permutations of one another have identical competitive advantages, we restrict our genome space to that of ordered dice. Thus, we disallow mutations that break the sorted nature of a genome. For instance, A may mutate to $(2, 3, 3, 3, 3, 6)$ but not to $(3, 2, 3, 3, 3, 6)$. In effect this accelerates the dynamics of our system, as most neutral competitions are avoided that would otherwise have to be settled by stochastic extinction. Further, naturally, it is universally better for a species to mutate up in sum rather than down. We set a fitness ceiling by only allowing mutations that keep $\sum_i X_i \leqslant n(n+1)/2$ (the sum of the standard die) and any $X_i \leqslant n$; the latter of which excludes a large of set of dice that are typically less competitive and allows efficient enumeration of the set of allowed dice.
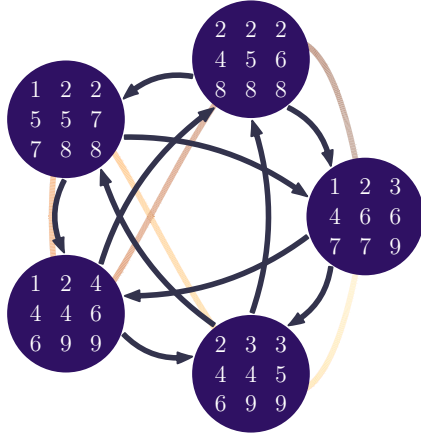
FIG. 1. The intransitive interaction of five nine-sided proper dice. Direction of the arrows indicate domination. The graph formed from the interactions has two Hamiltonian paths, one of which is indicated in the background. In other words, of the $4! = 24$ orderings of the dice, there are two that form an intransitive loop of dominance.

In total, we have thus created a mutation model where *universal fitness* can be measured, but where, occasionally, universally unfavorable mutations are preferred to adapt to coexistent competitors.

Instead of defining the interaction as a single roll of the dice, one might consider competitions of r rounds. As $r \to \infty$, any slight competitive advantage will result in certain overall wins. In this way, r can be chosen to control the ruggedness of the fitness landscape [3]. Here, we limit our attention to $r = 1$.

III. PROBABILITY OF INTRANSITIVITY

Before delving into the dynamics of the model, it is useful to have a feeling for the prevalence of intransitivity in random dice. Consider all dice such that $\sum X_i = n(n+1)/2$ and $1 \leqslant X_i \leqslant n$. Figure 2 shows the probability that k such dice contains at least one intransitive (Hamiltonian) k loop as
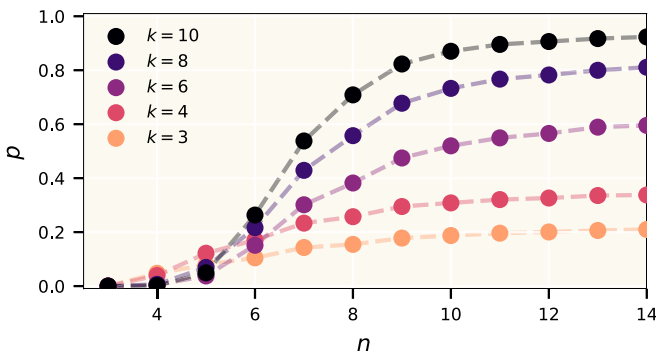

FIG. 2. Probability of intransitive (Hamiltonian) k loops in sets of k proper dice as a function of the number of sides n on the dice. Here, proper dice are sorted, has $\sum_i X_i = n(n+1)/2$ and $X_i \leqslant n$. A set of k dice $\{X_i\}$ has a k loop if an ordering σ exists such that $X_{\sigma_1} \prec X_{\sigma_2} \prec \cdots \prec X_{\sigma_k} \prec X_{\sigma_1}$. Each point is the result of averaging over 100 000 Monte Carlo samples with uniform probability for each valid die.

function of the number of sides of the dice n. The plot shows the fact that if you choose $k = 3$ random dice (with $n < 15$ sides), the probability that these dice interact intransitively is less than $\sim$20%. With a larger set of dice, not only do the probability of k loops increase, but so does probability of smaller sub-cycles (see Supplemental Material [31] for a version of Fig. 2 for loops of any size). In Fig. 2 we only consider a small number of dice, but very long intransitive cycles can also be found. For instance, in the set of $k = 910$ allowed nine-sided dice, the longest possible cycle is at least 891 (finding the precise length is NP-hard).

Thus, intransitivity is by no means rare, but (short) loops are not the norm either. However, in the dynamics of our model, it is much more unlikely for a species to go extinct in an intransitive loop than when species interact in a dominant manner. Thus, we expect one of two things to happen in the long run: the system will be taken over by one species or will be inhabited by a number of species that interact intransitively and show oscillations.

There is also a large heterogeneity in the advantages of the different dice. For instance, for $n = 6$, the die that has an advantage over most other dice is $(1, 3, 3, 4, 5, 5)$, beating on average $\sim$60 % of the other dice. The worst is $(1, 2, 2, 4, 6, 6)$, which is better than only $\sim$40 %. In contrast, the standard die $(1, 2, 3, 4, 5, 6)$ has precisely a 50 % chance of beating any other proper die. Similar conclusions can be made for all n.

We note that the precise statistics of Fig. 2 would be different if we considered not only proper dice, as some dice have many more permutations of their sides than others. The qualitative conclusions drawn would remain similar, nonetheless.

IV. FINITE MUTATION RATE UPHOLDS SPECIES DIVERSITY

Random, well-mixed ecosystems of many competing species interacting under demographic noise are unstable [32], and competitive exclusion often leads to a collapse to only a single or a few surviving species [33–35]. This, naturally, also applies to the present dynamical system. However, since the genome space of our model is not hierarchically organized, a finite mutation rate can induce a perpetual coevolutionary arms race.

One complication in counting the number of species in a system is due to the fact that the network of individuals is very unlikely to organize into fully connected components. This is a complication that is not unique to our system, but indeed any problem related to speciation [36]. For each pair of individuals, our genome distance rule specifies if they belong to the same species. Denote by C_i the number of individuals that individual i is considered the same species as (including i itself). An effective measure for species richness is then given by $S = \sum_i C_i^{-1}$. In the case of fully connected species, with no overlap between them, this measure coincides with simply counting the number of species. Likewise, we can define a species diversity measure that also accounts for evenness as $D = k^2(\sum_i C_i)^{-1}$. This is equal to the number of species only if each species occupy the same fraction of the entire system and thus small species contribute only negligibly to its value.
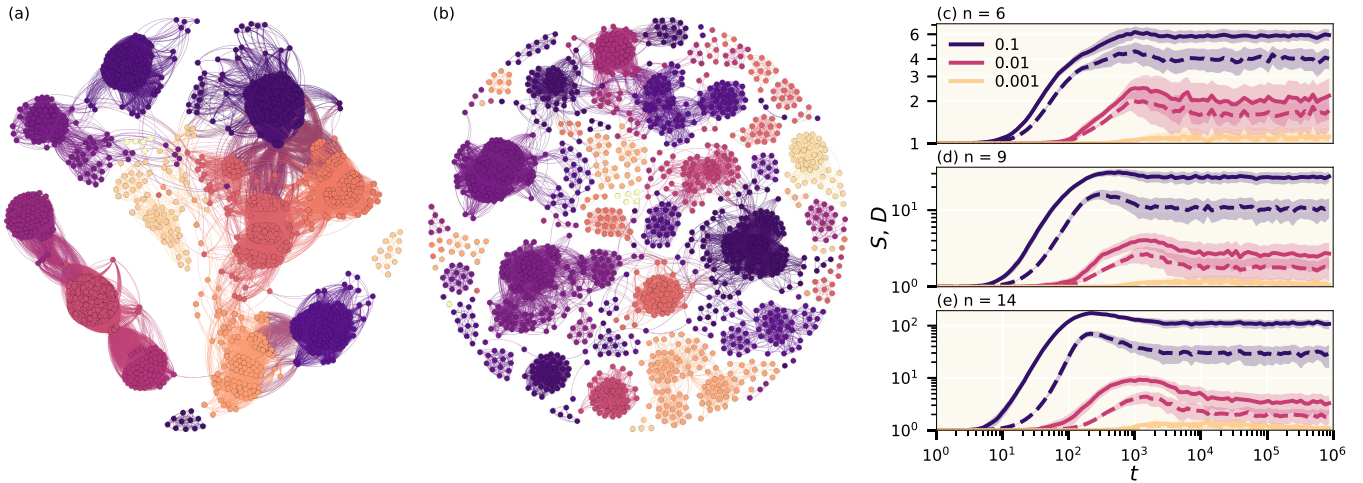
FIG. 3. Speciation. (a), (b) show 1 500 individuals of the system with links between them if they consider one another the same species. (a) has $n = 9$ and (b) $n = 14$, and in both cases $\mu = 0.1$. Nodes are colored, for visualization purposes only, using the Leiden community detection algorithm [30] on the undirected, unweighted graph. (c)–(e) show species richness S (solid lines) and diversity D (dashed) stabilizing in a simulations of varying genomic complexity n and mutation rate μ as indicated by the legend. Curves are averages over simulations with initial conditions of all dice equaling the standard die. All simulation were run with $\delta = 3$. $k = 10\,000$.

Figure 3 shows that both the mutation rate μ and the genome complexity n (dice size) set the number of species that a system of a certain size can maintain. At low mutation rates, the system is dominated by a small cloud of individuals that form a quasispecies [37], since, in this case, a single species can be locally dominant and no individuals can escape this local optimum at the low mutation rate.

At higher mutation rates, however, intransitive interactions appear and oscillatory dynamics of a high diversity system emerges. The systems have intransitive loops of many lengths, but the dynamics are dominated by short cycles ($\lesssim 5$ in the systems studied here). This is demonstrated and studied in the Supplemental Material [31] by considering the mean-field Lotka–Volterra equations of the system. In detail, the system behaves oscillatory with a frequency that remain relatively constant for multiple oscillation periods. On long time scales, however, stochastic events can change the dynamics, such as when a species in an intransitive loop stochastically goes extinct or when an individual suddenly mutates to dominate the existent intransitive interactions initiating a "*punctuated equilibrium*" event causing a sudden shift in oscillation frequency.

Figures 3(a) and 3(b) visualize species connectivity in the steady-state ecosystems that evolve from the dynamics of the model. In these graphs, an edge is drawn between two dice if they consider each other to belong to the same species. Despite starting with a single species, the system can evolve to one that has many species that are genomically disconnected. While no single measure can capture the complexity of these inter-species connections, running community detection algorithms on these graphs tend to find a number of clusters in the same order of magnitude as our richness S and diversity D measures. We note that for comparisons with other system sizes k, the values of the mutation rates should be rescaled accordingly, as the number of attempted mutation events per step is $\sim \mu k$. Thus, systems with a higher number of individu-

als can support high diversity in spite of having a low mutation rate per individual.

V. HETEROGENEOUS MUTATION RATES

Since a finite mutation rate is needed to maintain a finite diversity, we have an ecosystem collapse if the mutation rate is taken to zero. For instance, in a system of purely hierarchically interacting species, the dominant species will prefer a low mutation rate thus leading to a collapse of ecosystem diversity. In the present system, however, there is no global optimum, and a high mutations rate means quick adaptability and increases the chance of an individual to out-compete others by an evolutionary advantage. A high mutation rate is not strictly an advantage though, since it also means a high rate of bad mutation events towards either locally or globally worse genomes.

In Fig. 4 (inset), we show the competition between two populations with $\mu_A = 0.2$ and $\mu_B = 0.001$, respectively. For early times, a low mutation rate gives an advantage because there is a low rate of genomic decay and thus we see population B winning initially. This reflects the advantage of localizing a population around a local fitness maximum over more diffuse quasispecies at higher mutation rates [37]. However, at some point population A finds a competitive advantage over the slowly adapting population B and annihilates the latter completely. Varying μ_A and μ_B, the average outcome of these scenarios is shown in the main part of Fig. 4. The exact results depend on the initialization of the dice, but in this case, we see that $\mu \approx 0.1$ is generally advantageous.

We complete the design of our model by, finally, also permitting mutations in the mutation rate itself. In a hierarchical setting, this would lead to the immediate collapse of both the mutation rates and diversity. Figure 4 indicates, however, that in the present system there is also an advantage to having a finite mutation rate. Each panel in Fig. 5 show realizations of
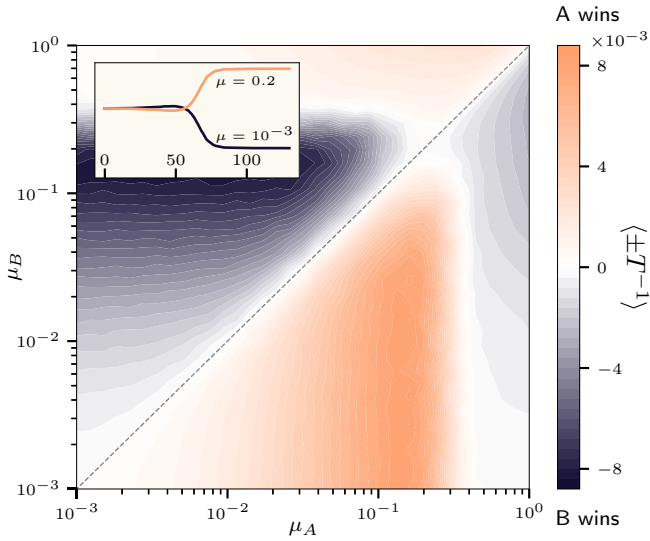
FIG. 4. Annihilation statistics of two populations with different mutation rates. Inset shows a simulation of $2 \times 10\,000$ dice with one half having $\mu_A = 0.2$ and the other $\mu_B = 0.001$. The time of annihilation of population B is $T = 130$ time steps. Main plot shows the average of $1/T$ measured with a negative sign if B wins. High values thus indicate that B tends to be annihilated and negative values that A tends to be annihilated. Values near zero indicate a system dominated by stochastic extinction or one where annihilation takes a very long time. All dice were initialized to $(1,1,1,6,6,6)$ at the beginning of the simulations.

a system of individuals, all initialized with the same genome and an initial mutation rate of $\mu = 0.01$. We observe two distinct outcomes: most trajectories reach a metastable state with a high mutations rate (die size $n = 6$ never reaches this state, but would do so if we instead started with initial $\mu = 0.1$, see Supplemental Material [31]), and some that decay towards zero mutation rates.

A characteristic of the metastable state is the rare but sudden decay events of both mutation rate and diversity of the entire system [Figs. 5(b) and 5(c)]. As the mutation rate decreases, it becomes less and less likely to escape the low diversity situation thereby creating a positive feedback loop for decreasing the mutation rate even further. Once collapsed, very large perturbations are needed to bring the system out of this situation. Even changing the mutation rate of half of the collapsed system to $\mu = 0.1$ is typically not enough to return to the high diversity state (see Supplemental Material [31]). In contrast, for the surviving high diversity ecosystems the average number of mutations that separate two random individuals is large. For instance, $\langle \sum_i |X_i - Y_i| \rangle_{X,Y} \approx 12$ for $n = 14$, which is about 2/3 of the average obtained between random dice.

VI. PERSPECTIVE

We have presented a theoretical model that, on the one hand, is exceedingly simple to define and, at the same time, successfully describes a host of complex phenomena related to coevolution. At fixed, finite mutation rates, the model permits a state of finite diversity in coevolutionary balance. For
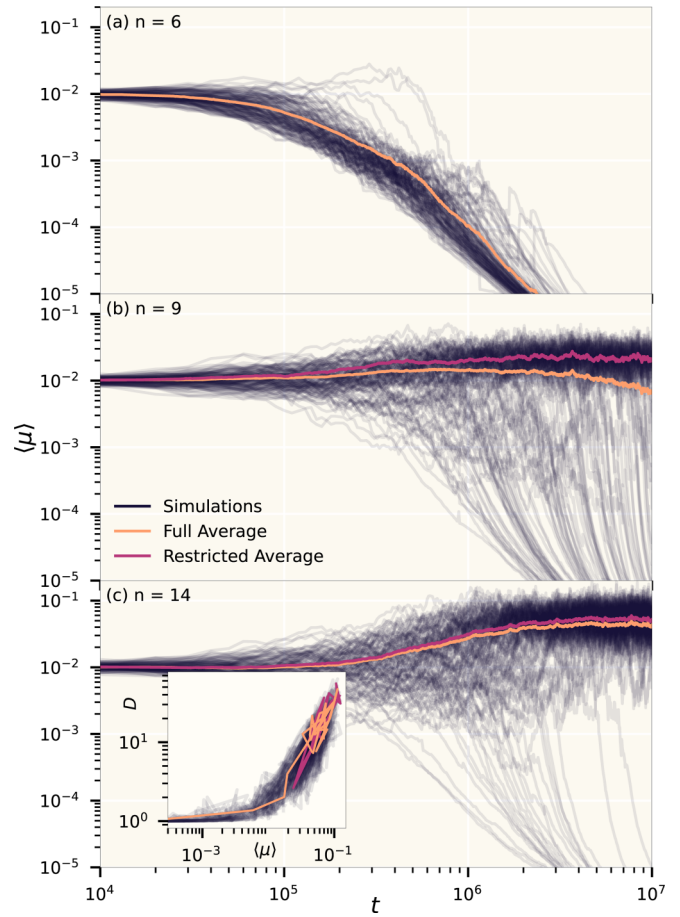

FIG. 5. Mutating the mutation rate. Simulations for which each individual mutates its mutation rate with a 1% chance of a 1% change per time step (Gaussian multiplicative noise). (a)–(c) Simulations for $n = 6$, 9, 14 showing the system average mutation rate $\langle \mu \rangle$ as a function of time steps. Orange lines show average over all simulations, whereas pink line shows an average over only those simulations that at $t = 10^7$ have $\langle \mu \rangle > 10^{-3}$. The full distribution of μ is narrowly peaked around $\langle \mu \rangle$ (see Supplemental Material [31]). Inset in panel (c) shows, for each realization, the average mutation rate versus the system diversity D (dark curves) for $t > 5 \times 10^5$, with two trajectories emphasized, one of which collapses towards $\langle \mu \rangle = 0$. All simulations use $\delta = 3$, but obtain similar results for other δ. The fraction of systems in the high mutation state depends greatly on initial mutation rate, even for the $n = 6$ die (see Supplemental Material [31]).

hierarchically interacting systems, allowing mutations in the mutation rates themselves will lead to an ecosystem collapse. In contrast, we find a metastable state of finite diversity, whose stability increases quickly with genomic complexity, measured by the number of sides of the dice n.

We only considered a well-mixed system, meaning that at all times each individual could meet any other individual. Introducing space to the model, e.g., putting the agents on a lattice, will most likely stabilize the observed effects even further; with spatial dynamics, intransitive relations will decay very slowly [22], and thus the rate of species extinctions decreases. Furthermore, speciation events should increase in frequency as space allows for transient allopatric speciation.

Precise quantification of intransitivity in the dynamical system is another interesting avenue for further research: despite being dominated by few intransitive cycles, a static view of the systems at any given time will not reveal the dominance of these cycles as at least one species will have a low population count due to the oscillatory Lotka–Volterra-like dynamics imposed by the dynamics of the intransitive loops.

In conclusion, from the simple rules of competing dice emerge a natural balance of mutation rates and diversity. Too high a mutation rate risks genomic decay and the disintegra-tion of quasispecies: "*mutate and die.*" Too few mutations are disfavoured in analogy to the Red Queen hypothesis: "*mutate or die.*"

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