This is a preproof accepted article for *Global Sustainability*

This version may be subject to change during the production process

DOI: 10.1017/ehs.2025.10015

Evolutionary Human Sciences (2025), **xx**, 1–24

ARTICLE TYPE

The Cultural Macroevolution of Arcade Video Games: Innovation, Collaboration, and Collapse

Sergi Valverde,[*†‡] Blai Vidiella,[¶] Andrej Spiridonov,[§] and R. Alexander Bentley[|0‡]

†Institute of Evolutionary Biology, CSIC-UPF, Pg. Barceloneta 37-49, Barcelona 08003, Spain

‡Center for the Dynamics of Social Complexity (DySoC), University of Tennessee, Knoxville, TN 37996, USA

¶Centre for Biodiversity Theory and Modeling, Theoretical and Experimental Ecology Station, CNRS, Moulis, France

§Department of Geology and Mineralogy, Vilnius University, Vilnius, Lithuania

|0Department of Anthropology, University of Tennessee, Knoxville, TN 37996, USA

*Corresponding author. Email: s.valverde@csic.es

Abstract

Arcade video games evolved in a constrained design space, following patterns of diversification, stabilization, and collapse that mirror macroevolutionary processes. Despite their historical significance and detailed digital records, arcade games remain underexplored in cultural evolution research. Drawing on a dataset of 7,205 machines spanning four decades, we reconstruct the evolutionary trajectories of arcade niches using a multi-scale framework that integrates trait-level innovation, genre-level selection, and systemic constraints. We identify two contrasting dynamics: (1) resilient genres—such as Fighter and Driving—maintained long-term viability through innovation and collaboration networks, while (2) early Maze and Shooter subgenres collapsed due to imitation and weak collaboration. Morphospace analysis reveals how technological traits—specifically CPU speed and ROM size—co-evolved with gameplay complexity, shaping the viable design space. We argue that genres operated as evolving cultural-ecological units—structured niches that shaped trait evolution through reinforcement, constraint, and feedback. This multi-scale perspective positions arcade games as a powerful model system for studying cultural macroevolution.

Keywords: Cultural evolution, Macroevolution, Arcade video games, Genre dynamics, Innovation, Collaboration Network, Scaling Laws, Technological constraints

Social media summary: Arcade game genres behave like cultural niches—some diversify, others become living fossils.

1. Introduction

What is an arcade video game? Although this may appear evident to experienced gamers today, video games lacked a clear cultural identity in their early years. It was uncertain whether they would be considered harmless amusement or a potential social concern, whether their audience would be primarily adults or children, and whether they would be perceived in positive, productive terms or as a moral and physical threat (Newman, 2018). This ambiguity reflects a broader pattern in cultural evolution: new technological and artistic forms do not emerge with predetermined meanings or functions but instead undergo a process of social negotiation and adaptation (Mesoudi, 2011).

Arcade video games developed within a distinct cultural and technological niche, separate from home consoles and personal computers (see Appendix A for a glossary of technical and cultural terms used throughout the paper). Unlike other gaming sectors, arcade games operated under a coin-operated model, where access was distributed among players rather than granted through direct ownership. This economic structure shaped the design of arcade games, favoring short, intense gameplay loops optimized for engagement and repeat play. As a result, the arcade game ecosystem evolved under unique constraints—balancing technological capacity, player psychology, and business incentives—that distinguish it from other forms of gaming.

Despite their significance, arcade games remain an underexplored domain in cultural evolution research. Most studies of technological evolution have focused on early human tools, industrial innovations, or modern software, while video gaming—which now involves over 3 billion players globally—has received limited attention from a cultural macroevolutionary perspective. Cultural evolution studies have explored traditional games such as Go (Beheim, 2025; Beheim et al., 2014), football (Mesoudi, 2020), and chess (Lappo et al., 2023), but arcade video games—despite their historical and technological richness—remain comparatively under analyzed. Beyond their narrative dimensions (Gilbert, 2019), video games evolve as complex cultural products (Lowood, 2009), shaped by technological constraints, market dynamics, and imitation pressures.

Arcade games, in particular, illustrate how economic structures, player behavior, and competitive pressures interact to drive innovation, persistence, and decline. Over time, they diversified into recognizable genres (Raessens & Goldstein, 2011)—such as maze games, shooters, fighting games, and driving simulators—each adapting to new technical affordances and shifting player expectations. As in other evolving systems, this diversification often followed a burst-and-collapse pattern (Žliobaitė et al., 2017), where early novelty gives way to saturation, redundancy, and decline.

This trajectory echoes dynamics observed in both biological and cultural evolution (Duran-Nebreda et al., 2024; Gould, 1974; Strotz & Lieberman, 2023), where an initial expansion phase is followed by contraction due to competition, imitation, and resource limitations. In this context, genres can be seen as culturally constructed niches that temporarily stabilize design conventions, coordinate expectations, and filter viable trait combinations. While some genres disappeared during periods of contraction, others persisted or even reemerged, suggesting the influence of cultural transmission mechanisms (Acerbi & Mesoudi, 2015; Boyd & Richerson, 1988; Henrich & Gil-White, 2001; Mesoudi, 2011). Prestige-biased transmission and structural reinforcement may have preserved dominant genre templates, giving rise to cultural "living fossils" (Eldredge & Stanley, 1984).

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

As Eldredge argued (DeGregori & Eldredge, 2020; Eldredge, 1985; Vrba & Eldredge, 1984), evolution reflects “the fate of transmissible information in an economic context”—a principle that applies directly to arcade video games, where cultural and market forces jointly determine which gameplay forms are retained, adapted, or abandoned. Rather than functioning as lineages in a phylogenetic tree, arcade genres may be better understood as evolving cultural-ecological systems—structured assemblages of games, developers, infrastructures, and player communities that co-evolve through interaction, competition, and feedback.

Here, we analyze the cultural and technological evolution of arcade video game genres by reconstructing diversification patterns, exploring technological scaling laws, and identifying collapse and resilience dynamics. Using the MAME (Multiple Arcade Machine Emulator) database, we extract detailed metadata on 7,205 arcade video games, including titles, manufacturers, release years, genre classification, and hardware traits (see Appendix B). Our study explores how arcade video games evolved through the interplay of innovation, collaboration, and constraint—investigating how certain genres adapted to changing conditions while others succumbed to stagnation. By tracing the evolutionary trajectories of arcade video games, we contribute to a broader understanding of how complex cultural systems diversify, persist, and collapse over time (Arthur, 2009; Valverde & Solé, 2006).

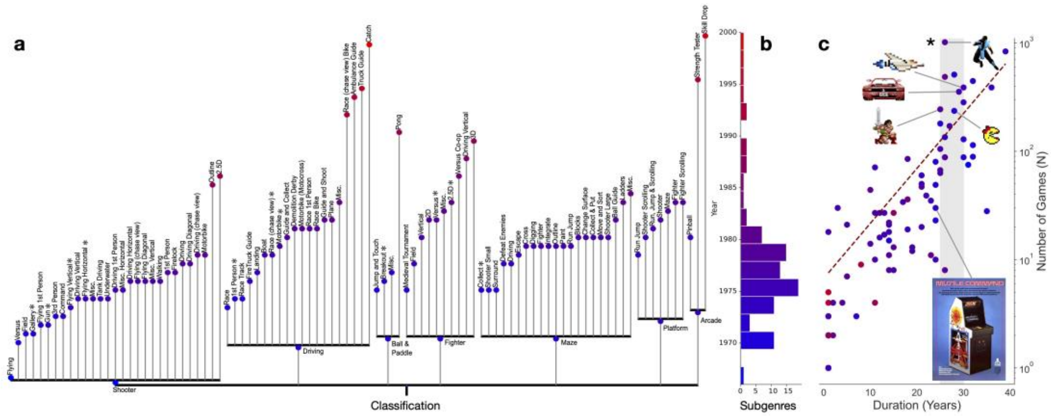

Figure 1. **Classification and diversity of arcade niches.** (a) Hierarchical map of arcade genres and subgenres ("niches"), showing their retrospective, culturally negotiated organization rather than a phylogeny (see text). (b) Niche expansion over time follows a “hat” pattern common in macroevolution—steady growth, a 1980s peak (the “golden age” of the arcade), and a long-tailed decline. (c) Subgenre size (number of games, N) scales exponentially with subgenre duration (dashed line shows best fit). Residuals highlight persistent outliers (gray area), notably Fighter/Versus (black asterisk), suggesting how cultural inertia and market feedback influences niche longevity. Game icons illustrate representative titles (from top to bottom): *Mortal Kombat* (Fighter/Versus), *Gradius* (Shooter/Flying Horizontal), *Out Run* (Driving/Chase View), *Rastan Saga* (Platform/Fighter Scrolling), *Pac-Man* (Maze/Collect), and *Missile Command* (Shooter/Command). Node color encodes year of first appearance (blue = early; red = recent).

2.Genres as Emergent Cultural Forms

Genres in arcade video games are not static taxonomies but emergent cultural-ecological forms, shaped through the iterative interactions of players, developers, and manufacturers. In the early years of arcade gaming, the identity of these machines was not self-evident: were they toys, competitive challenges, or technological spectacles? This uncertainty prompted open-ended exploration of gameplay possibilities,

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

producing a system of classification that evolved through cumulative social experience. As in other complex cultural domains, new genres emerged through modification and recombination of prior forms (Arthur, 2009; Hidalgo et al., 2007; Mesoudi & O'Brien, 2008; R. Solé & Valverde, 2020), eventually consolidating into partially stable niches within a broader design ecology.

To visualize this niche diversification process, we constructed a hierarchical map of genres and subgenres based on a community-defined classification of MAME games (see Figure 1). While panel (a) adopts a tree-like visual structure, it is not a phylogenetic tree in the biological sense. Each game is assigned both a main category (genre) and a subcategory (subgenre) by the community, reflecting gameplay features rather than historical descent. The resulting layout is better interpreted as a cultural classification—a map of gameplay modalities shaped by overlapping innovations, user conventions, and systemic feedback.

Main categories can be interpreted as broad gameplay templates, while subcategories reflect finer-grained innovations explored within those domains. Gameplay structures, like linguistic forms or film genres, emerge through shared expectations, aesthetic norms, and socially reinforced conventions (Reali & Griffiths, 2010; Sobchuk et al., 2024). These conventions function as cultural attractors—semi-stable tendencies toward particular forms in the cultural transmission process (see (Claidière et al., 2014; Sperber, 1996)—enabling both novelty and recognizability. The overlaps between genres reflect the recombinatorial and hybrid nature of arcade video game development—traits were not inherited strictly, but assembled modularly across shifting cultural and technological contexts.

Panel (b) in Figure 1 reveals a familiar "hat-shaped" diversification curve, widely observed in evolutionary and historical systems (Liow & Stenseth, 2007; Raulo et al., 2023; Valverde & Solé, 2015): a rapid expansion phase, peaking during the so-called "golden age" of arcade video games (Kent, 2010), followed by a protracted decline. This trajectory reflects a punctuated innovation, in which new gameplay forms rapidly emerged and diversified, followed by a period of saturation and structural slowdown as redundancy increased and external competition—such as the rise of home consoles—altered the entertainment landscape.

Importantly, genre decline did not manifest as an abrupt collapse, but rather as a gradual macroevolutionary tapering—similar to winnowing patterns seen in palaeobiological systems (Lloyd et al., 2012). After the peak, innovation slowed, niche consolidation intensified, and audience attention became more narrowly focused. While some niches faded quickly, others persisted—stabilized by institutional scaffolding, community practices, and genre-level reinforcement. This persistence suggests that long-term survival was shaped not only by intrinsic innovation potential but also by broader cultural-ecological dynamics, including social memory, market infrastructure, and transmission bias.

Panel (c) explores how the number of games per genre scales with genre lifespan. While most niches follow an approximately exponential trend—where longer-lived niches tend to accumulate more games—some, such as Fighter/Versus, persist far beyond these expectations. These long-lived outliers reflect not only ongoing innovation but also the effects of cultural prestige, infrastructure support, and brand loyalty. Their persistence highlights that survival in complex cultural systems depends on more than functional traits alone (Duran-Nebreda & Valverde, 2023; Gray et al., 2007); it is reinforced by the social dynamics, collaborative networks, and feedback loops that sustain niches.

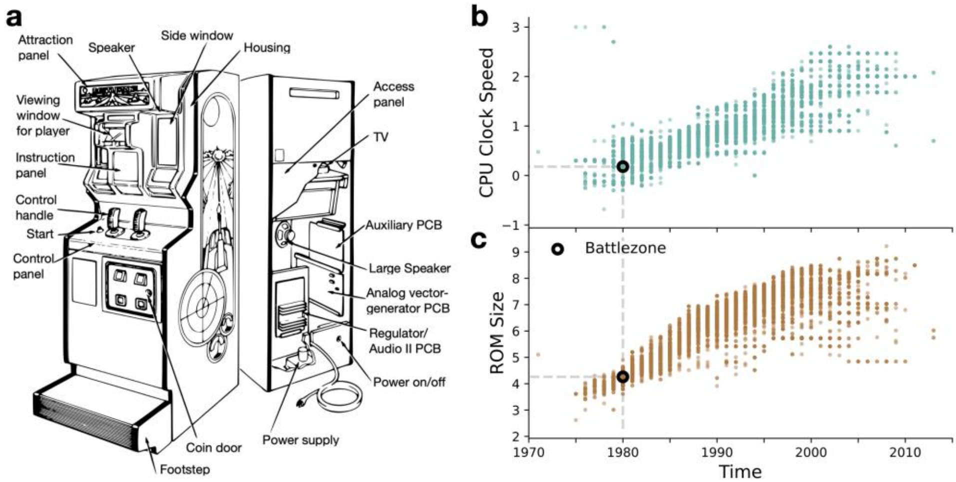

Figure 2. **Arcade video games are multi-trait cultural and technological products.** (a) Schematic of the *Battlezone* arcade system (Atari, 1980), a "Shooter/Tank Driving" game, illustrating both external and internal components. Adapted from Atari Inc.'s Operation, Maintenance, and Service Manual (1980), the front view highlights user interaction elements (e.g., control panel, viewing window), while the rear view reveals key internal hardware, including the Auxiliary PCB and Analog Vector-Generator PCB. (b, c) Temporal distribution of logarithmic CPU clock speed (b) and logarithmic ROM size (c) across arcade machines, demonstrating the increasing complexity of arcade hardware over time. The position of *Battlezone* within both distributions is marked (black dot).

3.The Morphospace of Arcade Games

Technological constraints play a pivotal role in shaping the evolution of complex cultural products (Basalla, 1988). Arcade video games are multi-trait cultural artifacts, integrating hardware, game mechanics, and interface design—each evolving under distinct market constraints and player expectations.

3.1Technological Constraints and Path-Dependent Evolution

A clear example of how hardware and gameplay co-evolve under constraint is Atari's *Battlezone* (1980), a shooter/tank driving game (Figure 2a). This machine employed a distinctive cabinet with both external and internal components that shaped user experience and game performance (Atkinson, 2021). On the outside, the player interacted with an Attraction Panel, Viewing Window, and Control Panel. Inside, custom hardware—such as the Auxiliary Printed Circuit Board (PCB) and the Analog Vector-Generator PCB—generated the game's characteristic vector graphics, creating a pseudo-3D tank battlefield (Wolf, 2012). This illustrates how hardware was not simply a technical limitation but also a creative driver of unique genre aesthetics, i.e., the now-iconic "retro" look.

To understand how hardware limitations shaped arcade game evolution more broadly, we focus on two consistently reported hardware traits: ROM size and CPU clock speed. These traits represent fundamental computational dimensions—storage and processing—and serve as proxy indicators of technological complexity. ROM (Read-Only Memory) stored all game assets–graphics, audio, and

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

executable code. Unlike RAM, ROM could not be modified during gameplay. Its capacity directly constrained the richness of content, animation complexity, and sound design. Equally important is the CPU (Central Processing Unit), which governs computational speed. For example, *Space Invaders* (Taito, 1978), which ran on an Intel 8080 microprocessor (see Box 1) clocked at 2 MHz, only 24 objects could be animated simultaneously. As the player eliminated enemies, the processing burden decreased—causing the game to speed up. What became a signature gameplay mechanic emerged directly from hardware limitations, not intentional design.

While technological capacity expanded over time (Figures 2b and 2c show log-transformed CPU speed and ROM size distributions), many games continued using outdated hardware. A horizontal band in Figure 2b, for instance, shows persistent use of 1 MHz CPUs well after more powerful chips became available. These choices were driven not only by cost, but by developer familiarity and compatibility with existing systems—creating path-dependent trajectories in technological evolution (R. V. Solé et al., 2013; Valverde, 2021).

Such patterns are consistent with Amdahl's Law (Amdahl, 1967), which states that improvements in system performance are limited by the slowest, non-parallelizable components. Even with faster CPUs, performance gains were constrained by serial processes like sprite rendering or audio synthesis. Consequently, developers often chose reliability and affordability over bleeding-edge architecture (Ashcraft et al., 2009). This partly explains why legacy hardware persisted across decades—and how technical constraints shaped the pace and direction of genre innovation.

Box 1. Microprocessors in Early Arcade Games: From Pinball to Space Invaders

The shift from electromechanical to digital arcade machines marked a pivotal transition in the evolution of video games. In the early 1970s, Bally Manufacturing collaborated with Dave Nutting Associates to embed Intel's 4004 CPU into pinball prototypes. While Taito's *Western Gun* (1975) still used discrete circuitry, its localized version—Midway's *Gun Fight*—became the first arcade game to use a microprocessor: Intel's 8080. This innovation enabled smoother animation and modular code reuse despite tight memory and processing limits.

These advances directly influenced *Space Invaders* (Taito, 1978), designed by Tomohiro Nishikado, who reused and extended *Gun Fight*'s architecture. The game's iconic mechanic—accelerating enemy motion—emerged from CPU limitations, as fewer on-screen invaders meant fewer calculations per frame. The huge success of *Space Invaders* triggered a flood of derivatives. Some were unauthorized bootlegs—hardware or software clones distributed without permission, often to bypass licensing restrictions. Others were licensed variants or early home adaptations like *Super Invader* for the Apple II. These versions highlight the blurred boundary between piracy, adaptation, and formal collaboration.

This genealogy illustrates how modular reuse, hardware constraints, and licensing partnerships enabled early innovation. In this article, we use "collaboration" to include both co-development and licensing agreements that facilitated the recombination of game mechanics, code, and hardware. These practices shaped the earliest arcade niches and established the evolutionary trajectories we trace in the broader analysis.

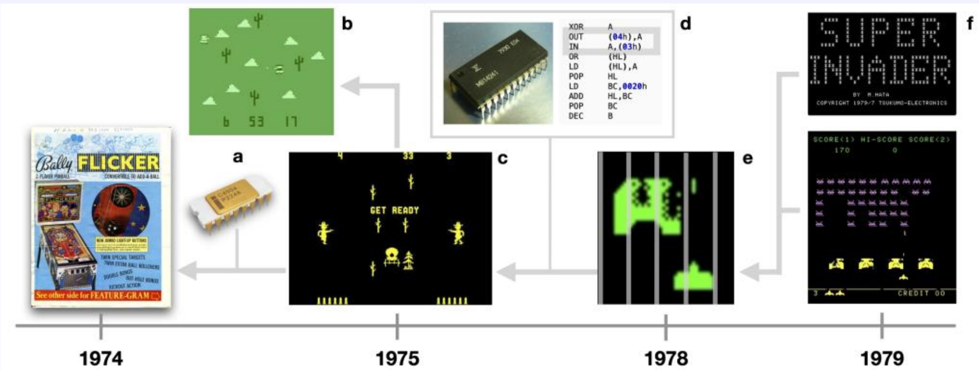

Figure 3. Hardware genealogy of early microprocessor-based arcade games. From Bally's *Flicker* pinball machine (a), to Taito's *Western Gun* (b), and Midway's *Gun Fight* (c–d), leading to Nishikado's *Space Invaders* (e), and its many clones and bootlegs (f). The highlighted assembly code routines were reused across games to animate sprites smoothly on a tile-based display (tile boundaries indicated by vertical grey bars in (e) were invisible in the actual game).

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

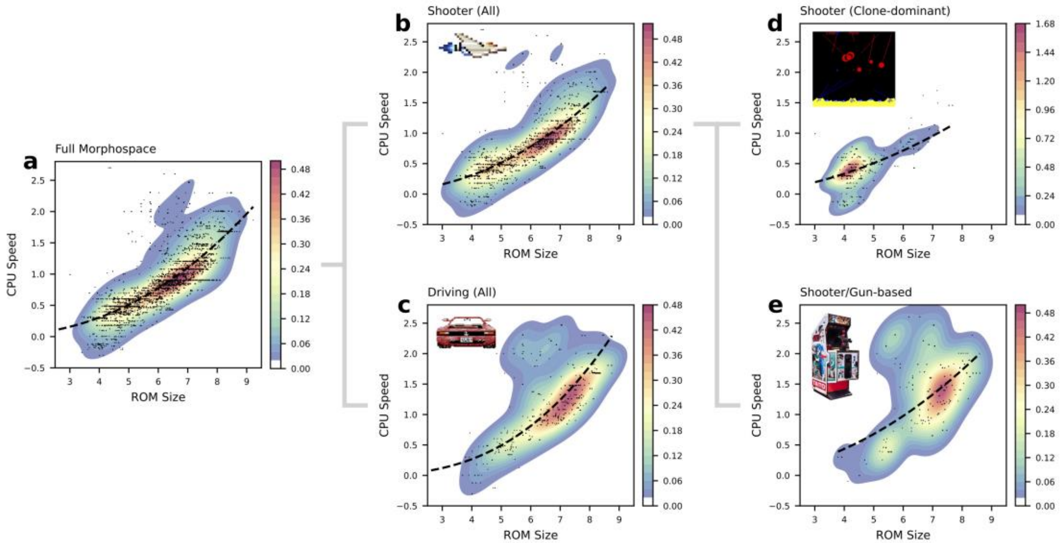

Figure 4. **Niche diversification in arcade game morphospace.** (a) Morphospace of arcade machines, defined by log-transformed CPU speed and ROM size. (b) The Shooter genre (N = 3,261) diversified into multiple subgenres, occupying both overlapping and distinct regions of the morphospace. (c) The Driving genre (N = 849) evolves into high-complexity regions, exemplified by multi-chip systems such as *Outrun*. Two density peaks in the Shooter genre reflect separate waves of game popularity: (d) Clone-dominant Shooters—such as *Missile Command* (inset) and *Space Invaders*—concentrate in lower-performance regions; (e) Gun-Based Shooters—such as *Operation Wolf*—shift toward higher ROM and CPU specifications, incorporating 3D graphics and immersive mechanics. Discontinuous trend lines indicate scaling relationships between CPU speed and ROM size, with niche-specific exponents (see main text).

3.2Scaling Laws Describe the Morphospace Trajectories of Arcade Niches

Although hardware constraints operated at the level of individual machines, they also shaped the broader evolutionary trajectories of arcade genres. To analyze these macroevolutionary patterns, we map games into a technological morphospace (McGhee, 1999; Raup & Michelson, 1965)—a conceptual design space defined by log-transformed CPU speed and ROM size (Figure 4a). Genres can thus be understood as occupying distinct regions of this space, reflecting their hardware demands and game design strategies.

Across the full arcade dataset, we observe a consistent power-law relationship between CPU speed (S) and ROM size (M):

$$S \sim M^{\alpha}, \tag{1}$$

where the exponent α quantifies how increases in memory capacity scale with processing requirements. If demands grew proportionally, we would expect $\alpha \approx 1$. Instead, we find super linear scaling across the dataset, with a global exponent of $\alpha = 2.3$, indicating that larger ROMs—enabling

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

richer content and compelling gameplay—typically generally required disproportionately faster CPUs to maintain performance.

The morphospace breakdown by genre and subgenre (Figure 4) reveals how these scaling exponents vary depending on gameplay mechanics. For example, Driving games—characterized by real-time physics, perspective changes, and customized hardware solutions—show the steepest scaling (a = 2.75, Figure 4c), reflecting high processing demands. Shooter games, in contrast, span a broad morphospace, enabled by their reliance on modular sprite-based rendering. They exhibit more moderate scaling (a = 2.28, Figure 4b), reflecting both diversity and standardization within the category.

Within niches, we also detect distinct waves of innovation. In the Shooter genre, morphospace density plots reveal two such peaks. The first, in the late 1970s and early 1980s, includes early shooters such as *Space Invaders* (see Box 1). Many of these early titles were widely imitated— "cloned" in arcade parlance—and relied heavily on pre-rendered visuals and standardized hardware, in contrast to the technical experimentation that defined later Shooter subgenres. They display a flatter scaling exponent (a = 1.88, Figure 4d), suggesting constrained technical evolution. A second wave, spanning the late 1980s through the mid-2000s, features Gun-based shooters such as *Operation Wolf*, which embraced faster processors, novel input devices (e.g., light guns), and immersive audio-visual design. These games expanded into higher-performance regions of the morphospace and exhibit steeper scaling (a = 2.0, Figure 4e), indicative of more sustained innovation.

Taken together, these patterns show that arcade evolution was not driven solely by stylistic shifts, but by trajectories through a landscape of material constraints. The scaling exponent in Equation 1 thus serves as a quantitative fingerprint of a genre's technological path—distinguishing between strategies of reuse and replication versus those of experimentation and refinement.

4.Imitation, Collaboration, and Niche Collapse

While the previous section explored how hardware constraints shaped genre viability through scaling dynamics, we now turn to the role of cultural and social mechanisms—particularly imitation, innovation, and collaboration—in determining long-term genre persistence or collapse (Duran-Nebreda et al., 2022; Henrich, 2016; Vidiella et al., 2022). As arcade technology advanced, cultural influences played a crucial role in shaping the evolution of genres, affecting not only the selection of games but also the way traits were combined, copied, or diminished over time.

Figure 5 displays three case studies on Maze, Platform, and Fighter games, each demonstrating unique evolutionary results influenced by these cultural forces. Maze games, typified by *Pac-Man* (1980) (Kent, 2010), reached a sharp peak in the early 1980s (Figure 5b). Platform games such as *Rastan Saga* (Taito, 1987) followed a slower, more gradual rise (Figure 5d), while Fighter games like *Mortal Kombat* (Midway, 1992) (Kocurek, 2015) sustained growth well into the 1990s (see Figure 5f).

Early Maze and Shooter subgenres of the 1980s were among the first to collapse under the weight of imitation. Landmark titles like *Pac-Man* and *Space Invaders* triggered a flurry of derivative development, spawning dozens of material clones and functional bootlegs (Markoff, 1981). This overproduction led to design redundancy and reduced trait diversity, undermining these genres' capacity for sustained innovation. Maze subgenres such as Driving, Collect, Shooter Small, and Outline exhibited particularly high bootleg prevalence (Figure 5b, inset), suggesting that copying became the dominant mode of transmission. These trends lend support the "dilution of expertise" hypothesis, where excessive copying without significant recombination results in cultural stagnation and eventual collapse (see Box 2).

Broader structural forces exacerbated this imitation-driven cultural collapse (Duran-Nebreda et al., 2022). In 1983, a home console crash and arcade industry downturn were system-wide failures caused by unsustainable early innovation. A feedback loop between arcades and home consoles destabilized the ecosystem: platforms like the Atari 2600 (Montfort & Bogost, 2009) and NES (Altice, 2015) eroded arcades' technological edge, while declining game quality and shifting consumer expectations accelerated the migration of both players and developers to home consoles. In contrast, many arcade Fighter games were cooperative projects in the 1990s (Figure 5f), where networks of collaboration brought together developers, manufacturers, and even players to facilitate sharing of information and drive innovation under growing competition.

The scaling of technology both influenced and restricted the evolutionary possibilities of arcade niches in unique ways. We use the exponent from Equation 1 to capture niche-specific technological trends—linking ROM size and CPU speed as a proxy for hardware-driven design complexity. Although all three genres in Figure 5 show power-law scaling in CPU speed and ROM size, they

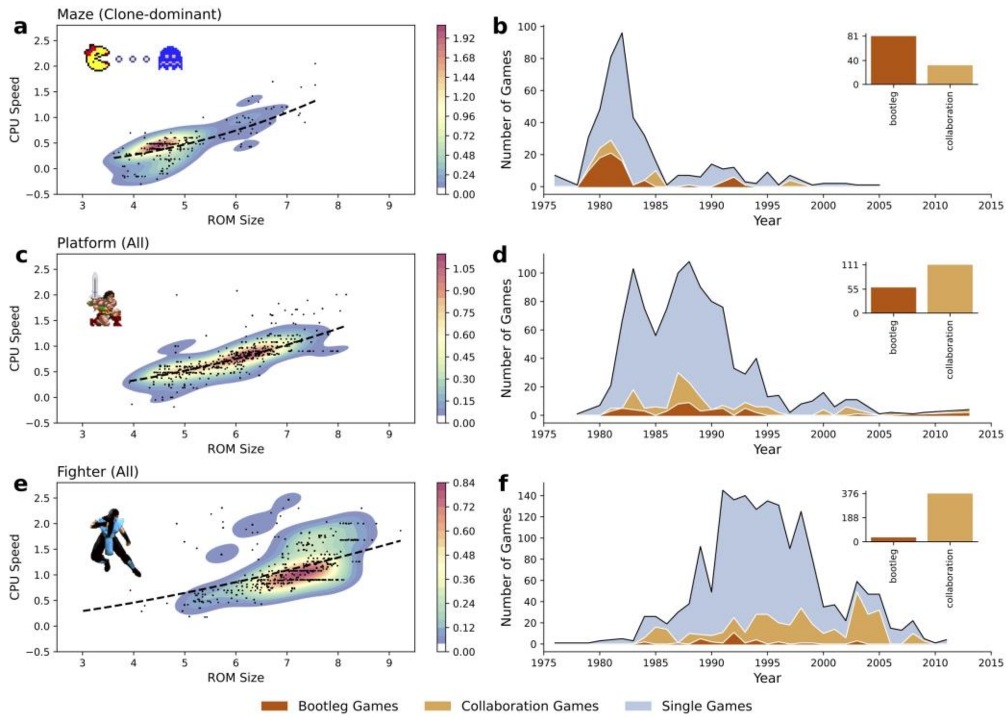

Figure5. Morphospace trajectories are shaped by the interplay of technological constraints, imitation, and collaborative innovation. Panels (a), (c), and (e) show the distribution of games within the morphospace for the Maze, Platform, and Fighter niches, respectively. The dashed lines indicate the fitted scaling relationship between log-transformed CPU speed (S) and ROM size (M), with exponents $\alpha = 2.5$ (Clone-dominant Maze subgenres), $\alpha = 2.02$ (Platform), and $\alpha = 1.55$(Fighter). Panels (b), (d), and (f) display the temporal distribution of game releases in each genre. The area under each curve represents the number of games released per year, with color-coding indicating single-developer games (blue), bootlegs (brown), and collaborative productions (gold). Inset bar charts summarize the proportion of game types per genre, highlighting the prevalence of imitation versus collaboration.

have different exponents. Maze games show steep scaling (α = 2.5), pushing technical limits—for example, the computational demands of sprite management and AI pathfinding—but did not sustain

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

novelty (Figure 5a). By contrast, the computational demands of Fighter games scaled more modestly (a = 1.55), suggesting steady innovation focused on gameplay refinement, such as prioritizing fluid input responsiveness and rich character animations, rather than brute-force processing throughput (Figure 5e).

Overall, arcade trends unveil a macroevolutionary process: niches did not simply decline in popularity but collapsed due to imitation limiting their innovation potential. Resilient niches, on the other hand, succeeded not just by producing new variants, but by channeling novelty into cumulative innovations—through refinement, trait recombination, and coordinated exploration. In robust cultural evolution, it's not the volume of novelty that matters—but how it's organized.

Box 2. The Dilution of Expertise Hypothesis

A central hypothesis in our study is that excessive imitation, when not balanced by innovation or recombination, destabilizes cultural systems (i.e., the *dilution of expertise* hypothesis (Duran-Nebreda et al., 2022)). When imitation outpaces a system's capacity to generate or integrate new traits, expertise becomes diluted. New entrants replicate existing solutions without fueling the recombination that drives long-term innovation. Trait diversity saturates, performance plateaus, and the system enters decline.

In our arcade dataset, we approximate this structural shift using two indicators: the number of bootleg games (unauthorized clones or direct copies) and the number of collaborative games (co-productions between developers, licensors, or distributors). A genre is considered in collapse when bootlegs exceed collaborative projects over time—signaling a transition from recombination to saturation, as observed in the decline of early Maze and Shooter subgenres.

To formalize this process, we define a simple model in which trait diversity $V(N)$ depends on the balance between imitation and collaboration. Let $B(N)$ and $C(N)$be the cumulative number of bootleg and collaborative games. Then:

$$\frac{dV}{dN} = \alpha \left(1 - \frac{B(N)}{B(N) + C(N)}\right)^{\beta} \sim \left(\frac{C(N)}{B(N) + C(N)}\right)^{\beta}$$

Here, α is the baseline innovation rate, and $\beta \geq 1$controls sensitivity to imitation. When bootlegs dominate, the imitation ratio $B/(B + C)$approaches 1, suppressing diversity growth. When collaboration prevails, diversity increases steadily.

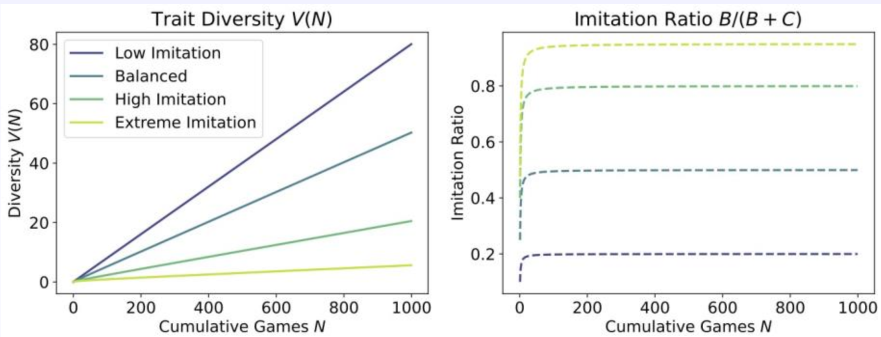

Figure 6. Simulated trait diversity and imitation ratio dynamics. Left: trait diversity $V(N)$under varying imitation-to-collaboration regimes. Right: imitation ratio $B/(B + C)$ over time. In high imitation scenarios, diversity saturates rapidly.

These simulations capture how cultural diversity responds to shifting imitation regimes. In "Low Imitation" scenarios, diversity grows almost linearly. As bootlegging rises, diversity slows and eventually plateaus—reflecting recombinant collapse. This dynamic helps explain why genres like Fighter and Driving games sustained innovation: not via sheer volume, but through recombination of diverse expertise.

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

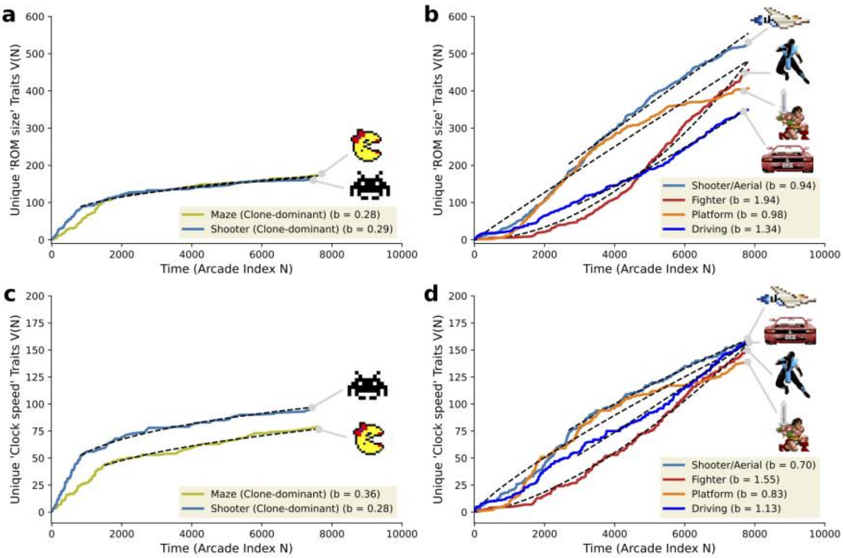

Figure 7. **Scaling of trait diversity in collapsing (left column) and diversifying (right column) arcade genres.** Panels (a) and (c) show the sublinear accumulation of unique ROM and CPU configurations in Maze (Figure 5a) and Shooter (Figure 4d–e) subgenres, consistent with low scaling exponents ($b < 0.4$) and limited design exploration. Panels (b) and (d) show that Fighter, Platform, and Driving games achieved higher trait diversity with increasing game output, reflecting sustained recombination and innovation. Dashed lines represent the fitted power-law relationship between trait diversity ($V(N)$) and the total number of games (N), with exponents b indicating genre-specific evolutionary potential (see text).

5.Avoiding Collapse through Combinatorial Innovation

In this section, we explore how recombination enabled resilient niches to explore design space more effectively—through increased trait diversity. Combinatorial innovation is not only technical but cultural, emerging most readily in niches where collaboration was strongest (as suggested in Section 4). Interactions among manufacturers, developers, and players provided the organizational infrastructure needed to mix, adapt, and refine traits across games.

To study the link between collaboration and innovation, we analyze the temporal diversity of two core technological traits—ROM size and CPU clock speed—across a range of arcade niches. As shown in Figure 7, we track the accumulation of unique ROM and CPU configurations, denoted $V(N)$, as a function of the total number of games N in each genre. Following established models (Egghe, 2007), we expect trait diversity to follow a power-law relationship (see Box 2):

$$V(N) \sim N^b \tag{2}$$

where the exponent b serves as a signal of evolutionary potential. Sublinear values ($b < 0.5$) indicate redundancy and limited exploration, while linear or super linear scaling ($b \geq 1$) reflects ongoing innovation under a combinatorial regime.

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

This scaling framework suggests the recombination mechanisms that enabled niches to withstand the broad decline of arcades in the 1980s, subsequently thriving during the revival of the 1990s. Maze and Shooter games were early commercial hits, however several of their subgenres showed high sublinear rise in trait diversity ($b \approx$ 0.28-0.36), indicating imitation-driven collapse. Despite continued production, a lack of novel gameplay and technical variation led to player fatigue and genre stagnation. Bootlegging and imitation—previously identified as a contributor to collapse (Figure 5)—accelerated these trends by disincentivizing experimentation.

Not all subgenres followed the same trajectory. Within Shooter games, for instance, the Aerial Combat subgroup (see Appendix B) maintained higher CPU diversity ($b \approx$ 0.69), avoiding collapse through innovations in scrolling mechanics, enemy AI, and free movement. This case shows that access to improved hardware was not sufficient on its own—what mattered was the ability to recombine existing elements into meaningful new forms (Arthur, 2009; Juul, 2011; Koppl et al., 2023).

By contrast, niches such as Fighter, Platform, and Driving sustained innovation through collaboration and shared development networks during the 1990s (see Box 3). Fighter games displayed the steepest increase in trait diversity ($b \approx$ 1.54–1.94), integrating innovations across hardware, animation, and input mechanics. This pattern suggests a process of combinatorial innovation, in which existing elements were reassembled into novel configurations—enabled in part by collaborative design practices and interoperable platforms. Platform and Driving games followed with moderate-to-high values ($b \approx$ 0.98–1.34), suggesting distinct but viable innovation strategies: Platformers emphasized gameplay mechanics and interactive environments, while Driving games pushed realism through technical advances in vehicle physics and AI complexity.

These findings reinforce the deeply path-dependent nature of cultural and technological evolution: once a niche becomes entrenched in an imitative regime, its capacity to innovate—and survive—is sharply reduced. Niches with low b values are geometrically restricted in morphospace, confined to narrow corridors of viable configurations defined by underlying trait-scaling constraints (see Appendix C). What may appear as steady technical progress can, in fact, mask a hidden contraction in the diversity of design options—a signature of trait canalization that links cultural collapse to structural constraint.

Box 3. Recombination and Collaboration Networks Fostered Arcade Resilience

The 1990s marked a pivotal shift in the arcade industry. After the saturation and collapse of early Maze and Shooter subgenres, a new wave of games emerged that recombined hardware, gameplay mechanics, and cultural references. These machines did more than upgrade components—they restructured the logic of arcade entertainment. Three niches exemplify this transition, each occupying a distinct region of the morphospace with unique combinations of CPU speed, ROM capacity, and peripheral innovation (see Figure 8). Their success reflected combinatorial innovation supported by collaboration networks that spanned both technical and organizational domains.

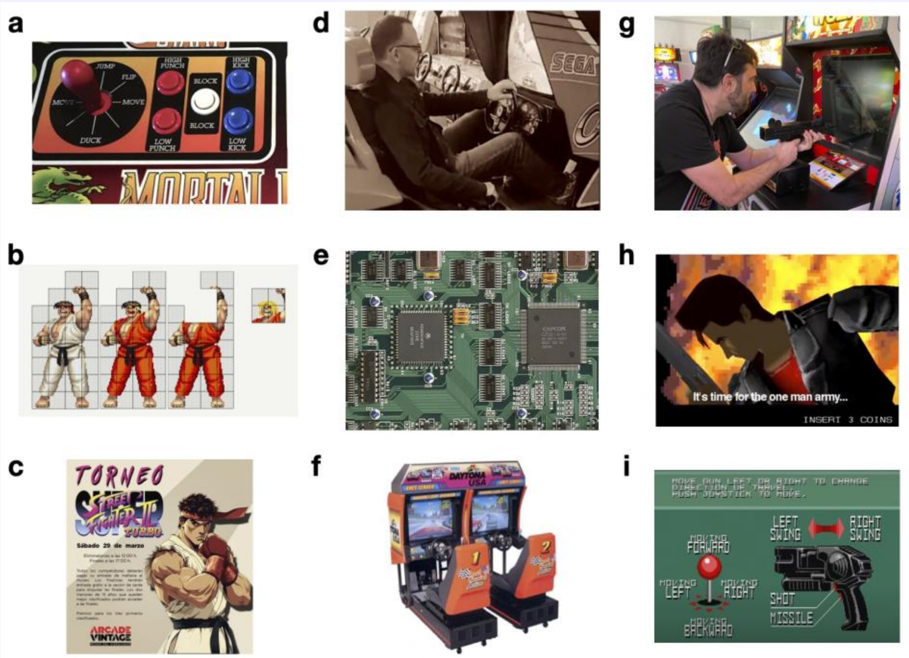

Figure 8. Gameplay and hardware innovations in the 1990s across three resilient arcade genres.

- **Fighter/Versus games**—such as *Street Fighter II* (Capcom, 1991) and *Mortal Kombat* (Midway, 1992) standardized six-button layouts (a), enabled combo mechanics, and scalable animation pipelines to support large sprite libraries (b). Competitive communities and tournament circuits reinforced mastery and prestige (c), anchoring these games in durable brand ecosystems. Underlying hardware platforms like Capcom's CPS-1 and CPS-2 supported higher ROM capacity and advanced sprite handling.
- **Driving games**, including *Daytona USA* (Sega, 1994), introduced analog steering and force-feedback controls for immersion (d), powered by multi-board CPU systems capable of running real-time graphics and physics simulations independently (e). Multiplayer modes emerged via networked cabinet setups (f), reinforcing repeat play and social engagement.
- **Shooter/Gun games**—exemplified by *Time Crisis* (Namco, 1995—blended cinematic pacing with physical light-gun targeting (g), often housed in immersive, enclosed cabinets. Narrative-driven shooter design emerged through time-based scenarios (h), while games like *Operation Gunbuster* (Taito, 1992) introduced branching level structures and free-roaming spatial exploration (i), enabling replayability and genre hybridization.

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

6. Discussion

Understanding how and why cultural traits persist, diversify, or disappear is central to cultural evolution research (Enquist et al., 2024; Zhang & Mace, 2021). The case of arcade video games—rich in technical constraints, cultural feedback, and aesthetic conventions—offers a powerful model system for studying how innovations emerge, stabilize, or collapse under selective pressure. Figure 9 synthesizes our findings into a multi-scale framework of arcade game evolution, highlighting feedback loops between trait-level dynamics, genre-level selection, and the broader cultural ecology. Rather than a linear process, genre persistence emerges through multi-level interactions shaped by the interplay of technological constraints and social reinforcement.

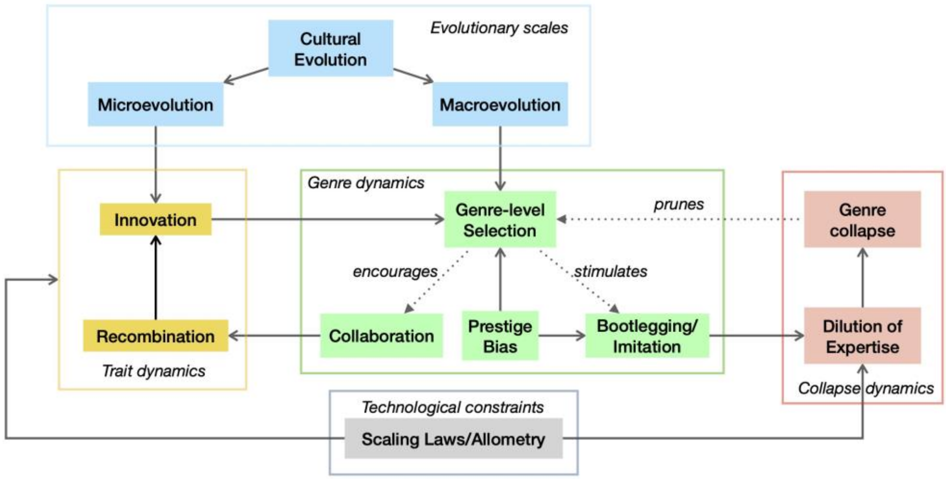

Figure9. **A multi-scale framework for cultural evolution in arcade games.** Genres are modeled as higher-level cultural-ecological units that mediate between innovation, persistence, and collapse across four interacting domains: (1) *Trait Diversification* (gold, left) captures microevolutionary novelty via innovation and recombination; (2) *Genre Dynamics* (green, center) represent macroevolutionary reinforcement, niche structuring, and selection; (3) *Collapse Dynamics* (red, right) reflect the erosion of genre integrity through imitation and dilution of expertise; (4) *Technological Constraints* (grey, bottom) ground the system through scaling laws that constrain viable innovations. Solid arrows indicate causal influences; dotted lines denote feedback and filtering. Together, these processes illustrate how multi-scale feedback loops shape cultural evolution in arcade games (see text).

6.1Trait Diversification: Innovation, Scaling, and Modularity

At the microevolutionary level, arcade novelty emerged from the interaction between innovation, recombination, and technical feasibility. As shown in the left (gold) portion of Figure 9, two major forces shaped trait diversification: hardware constraints and creative reuse. Innovations in animation fluidity, control responsiveness, or AI behavior were tightly bounded by CPU speed and ROM size. These parameters defined not just the limits of performance but the design space itself—what could be rendered, stored, or executed in real time.

Our analysis reveals that arcade evolution followed robust scaling laws between CPU and ROM capacity (Equation 1), suggesting that constraints were not merely limits but structuring forces. These scaling relationships resemble biological allometries (Brown et al., 2004; West et al., 1997), where functional traits co-vary along developmental axes (Evans et al., 2021; Gould, 1974). In cultural systems,

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

such allometric relationships can induce canalization—restricting trait variation along a constrained manifold despite underlying diversity.

Despite these constraints, creativity can thrive through reuse. Designers frequently hybridized existing mechanics, forming novel gameplay configurations from prior templates. This reflects how cultural change, unlike genetic mutation, often proceeds through the recombination of known elements (Boyd & Richerson, 1988; Koppl et al., 2023; Valverde & Solé, 2015). Rather than inventing from scratch, designers exploited modularity, allowing new forms to emerge within existing limits.

6.2Genre Dynamics: Selection, Prestige Bias, and Collaboration

While trait-level innovation occurred locally, long-term viability was determined at the genre level. Genres acted as higher-order cultural entities that filtered and stabilized viable traits. As shown in the central (green) portion of Figure 9, genre categories did not emerge solely from gameplay mechanics, but from a combination of community recognition, industrial reinforcement, and narrative framing (Therrien, 2015).

In this framework, genres resemble "species" in biological macroevolution (Eldredge, 1979; Stanley, 1975): they define selective regimes, constrain novelty, and scaffold persistence. Our findings show that genres with strong networks—such as Fighter games, supported by tournaments, social visibility, and co-development—exhibited greater resilience. These genres accrued prestige and cultural capital, becoming entrenched through player endorsement and competitive play (Henrich & Gil-White, 2001; Kocurek, 2015).

Conversely, niches dominated by imitation but lacking collaboration were more vulnerable to collapse. Bootlegging, while initially facilitating diffusion, ultimately eroded genre integrity by flooding the ecosystem with redundant and lower-quality clones—a process we describe as “dilution of expertise.” This phenomenon, highlighted in Table 1, is not just a social effect but also the downstream outcome of scaling-induced constraints on trait diversity (see Figure 9).

6.3 Collapse Dynamics and Feedback Loops: Dilution, Stagnation, and Reemergence Genre collapse often resulted not from technological obsolescence but from ecological saturation and cultural exhaustion. As illustrated in the right (red) portion of Figure 9, early Maze and Shooter games underwent rapid proliferation followed by stagnation and decline—a rise-and-fall pattern typical of reduced innovation. Once a design space was thoroughly explored, novelty diminished and attention shifted elsewhere.

This collapse was frequently compounded by low collaboration. Our analysis of development metadata shows that genres with more collaborative projects sustained higher trait diversity and longer persistence. In contrast, genres dominated by isolated or bootleg production showed reduced innovation and faster decline. Cultural niches can fail not only from under-performance but also from overexposure and creative fatigue.

Importantly, cultural collapse was not always terminal. Several subgenres, such as multidirectional shooters (e.g., *Gun Fight*), reemerged decades later, often facilitated by new technologies and cultural shifts (Ke et al., 2015). Elements of once-dormant genres can recombine and reassert themselves, much like latent developmental pathways in biology (Barnett et al., 2025). These punctuated dynamics are consistent with macroevolutionary patterns observed in both biological and cultural systems (Duran-Nebreda et al., 2024).

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

6.4Synthesis: Cultural Evolution Beyond Games

Bringing these dynamics together, Figure 9 presents a conceptual model in which traits, genres, constraints, and collapse interact across multiple scales. Trait innovation arises through recombination and technical feasibility; genres filter and reinforce viable forms; collapse results from oversaturation or dilution of expertise. These components interact through recursive feedback loops: bottom-up innovation reshapes genres, which in turn constrain future developments.

At the center of this framework is the concept of genre—not as a static category, but as a culturally constructed niche shaped by interaction among developers, players, infrastructure, and markets. Rather than fixed taxonomies, we treat genres as evolving macro-units, comparable to geobiomes or palaeobiological systems defined by temporal and ecological boundaries (Spiridonov & Eldredge, 2024). Genres maintain coherence through constraint and recombination, even as their internal configurations shift over time.

This perspective resonates with broader models in cultural macroevolution (Mesoudi, 2011; Turchin & Gavrilets, 2021), where higher-order cultural forms—like styles, traditions, or technological paradigms—shape the evolutionary landscape of lower-level traits. It also echoes theories of downward causation (Tëmkin & Eldredge, 2007), in which emergent structures guide the viability of their parts. In arcade evolution, genres served this role, influencing which traits were retained, recombined, or abandoned—and thereby steering the very shape of cultural possibility.

A closely related perspective is offered by Cultural Attraction Theory (CAT) (Claidière et al., 2014; Sperber, 1996), which emphasizes the constructive nature of cultural transmission. According to CAT, the stability of cultural traits can arise not through faithful copying, but through recurrent transformation that converges probabilistically on preferred forms—so-called cultural attractors. These attractors represent statistical regularities in the cultural landscape, shaped by psychological, contextual, and ecological biases.

While our model shares CAT's focus in how convergence shapes cultural form, the arcade ecosystem reveals a contrasting dynamic: under conditions of high constraint and market saturation, excessive fidelity—rather than transformation—can become maladaptive. Genres overwhelmed by nearly identical clones lost distinctiveness, leading to cultural fatigue and collapse. This suggests that in certain morphospaces, imitation is not merely insufficient (as CAT proposes), but can actively undermine diversity and resilience. Stability and breakdown may both result from convergence, but through different mechanisms: one via reconstructive attraction, the other via preservative redundancy.

Arcade games, then, offer more than nostalgia or entertainment—they provide a model for how cultural evolution unfolds under constraint, hierarchy, and feedback. The fragility of imitation, the resilience of modularity, and the structuring role of genres are patterns that recur across domains—from software to science. By formalizing these dynamics, we move toward a general theory of cultural macroevolution—one that accounts not just for the tempo and mode of innovation, but for the architecture that sustains it.

Acknowledgments We thank our colleague Josep Sardanyés for his critical review of our article, and the technical assistance of Eduardo Arancibia, curator of the Arcade Vintage Museum (Ibi, Alicante, Spain), Tomás García-Merás (Recreativas.org), and the director of the Arcade Vintage Museum, José María Litarte.

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

Author Contributions S.V., A.S., and R.A.G. conceptualized the study. S.V. developed the methodology and curated the data. B.V. and S.V. handled data visualization. S.V., R.A.B., and A.S. contributed to writing. All authors reviewed and approved the final submitted draft.

Financial Support SV was supported by the grant PID2020-117822GB-I00, funded by the Ministerio de Ciencia, Innovación y Universidades (MICIU) / Agencia Estatal de Investigación (AEI) / 10.13039 / 501100011033. AS was supported by the grant S-MIP-24-62 BretEvoGeneralized.

Conflicts of Interest The Author S.V., B.V., A.S., and R. A. B. declare none.

Research transparency and reproducibility All data processing scripts, model code, and analysis notebooks used in this study are publicly available in the GitHub repository: https://github.com/ svalver/arcade-macroevolution. This includes scripts to reproduce all main text and supplementary figures, as well as the complete scaling table of genres and subgenres.

Data availability statement The dataset analyzed in this study was derived from metadata collected through the MAME project (https://www.mamedev.org), an open-source emulator dedicated to preserving the history of arcade video games. The curated dataset used in our analysis—including game traits, genre structure, and collaboration labels—is available in CSV format in our GitHub repository at https://github.com/svalver/arcade-macroevolution.

Table 1. Comparative analysis of arcade game niches, examining imitation, the role of collaboration, and scaling exponents a (a proxy for technical complexity) and b (trait diversity). Low b values indicate redundant designs, while high b values reflect sustained diversification. Successful niches avoided cultural collapse through creative recombination and collaborative openness, rather than solely increasing technical capacity.

Niche	Imitation	Collaboration	Complexity	Diversity	Gameplay
Maze (Clone-dominant)	High imitation, extensive bootlegging led to redundancy and stagnation.	Weak collaboration and isolated development ecosystems.	$a = 2.50 \pm 0.33$	$b \approx 0.28 - 0.36$	Simple maze navigation and chase mechanics with little innovation beyond early successes like *Pac-Man*.
Shooter (Clone-dominant)	High imitation with repetitive design loops.	Fragmented development; few cross-studio innovations.	$a = 1.88 \pm 0.27$	$b < 0.4$	Repetitive enemy waves and predictable scrolling patterns; minimal progression in AI or physics.
Shooter (Aerial Combat)	Moderate imitation but with greater design variation.	Moderate collaboration; some modular design reuse.	$a = 2.17 \pm 0.09$	$b \approx 0.69 - 0.94$	New movement styles, improved enemy behaviors, and visual upgrades extended the niche lifespan.
Platform	Moderate imitation with adaptive innovation.	Increasing collaboration across studios, enabling adaptive innovation.	$a = 2.02 \pm 0.11$	$b \approx 0.61 - 0.98$	Transition from simple jumping to multi-directional movement and physics-based interactions.
Fighter	Strategic imitation combined with high recombinant innovation.	High collaboration and multi-studio development ecosystems.	$a = 1.55 \pm 0.13$	$b \approx 1.54 - 1.94$	Diversified movesets, combo systems, counters, and refined input mechanics; genre supported competitive play.
Driving	Low imitation, strong emphasis on technical experimentation.	Strong collaborative environments, often tied to hardware-specific innovation.	$a = 2.75 \pm 0.24$	$b \geq 1$	Expanded realism via vehicle physics, environmental detail, and increasing track and AI complexity.

References

Acerbi, A., & Mesoudi, A. (2015). If we are all cultural darwinians what's the fuss about? clarifying recent disagreements in the field of cultural evolution. *Biology & philosophy*, *30*, 481–503.

Altice, N. (2015). *I am error: The nintendo family computer/entertainment system platform*. MIT Press.

Arthur, W. B. (2009). *The nature of technology: What it is and how it evolves*. Simon; Schuster. Atkinson, P.

(2021). Atari design: Impressions on coin-operated video game machines.

Barnett, M., Meister, L., & Rainey, P. B. (2025). Experimental evolution of evolvability. *Science*, *387*(6736), eadr2756.

Basalla, G. (1988). *The evolution of technology*. Cambridge University Press.

Beheim, B. A. (2025). Opening strategies in the game of go from feudalism to superhuman ai. https://doi.org/10.31234/osf.io/cewst_v1

Beheim, B. A., Thigpen, C., & Mcelreath, R. (2014). Strategic social learning and the population dynamics of human behavior: The game of go. *Evolution and Human Behavior*, *35*(5), 351–357.

Boyd, R., & Richerson, P. J. (1988). *Culture and the evolutionary process*. University of Chicago press.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Claidière, N., Scott-Phillips, T. C., & Sperber, D. (2014). How darwinian is cultural evolution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1642), 20130368.

DeGregori, J., & Eldredge, N. (2020). Parallel causation in oncogenic and anthropogenic degradation and extinction. *Biological Theory*, *15*(1), 12–24.

Duran-Nebreda, S., Bentley, R. A., Vidiella, B., Spiridonov, A., Eldredge, N., O'Brien, M. J., & Valverde, S. (2024). On the multiscale dynamics of punctuated evolution. *Trends in Ecology & Evolution*.

Duran-Nebreda, S., O'Brien, M. J., Bentley, R. A., & Valverde, S. (2022). Dilution of expertise in the rise and fall of collective innovation. *Humanities and Social Sciences Communications*, *9*(1), 1–10.

Duran-Nebreda, S., & Valverde, S. (2023). The natural evolution of computing. In *The oxford handbook of cultural evolution*.

Egghe, L. (2007). Untangling herdan's law and heaps' law: Mathematical and informetric arguments. *Journal of the American Society for Information Science and Technology*, *58*(5), 702–709.

Eldredge, N. (1979). Alternative approaches to evolutionary theory. *N. Bull. Carnegie Mus. Nat. Hist.*, *13*, 7–19.

Eldredge, N. (1985). *Unfinished synthesis: Biological hierarchies and modern evolutionary thought*. Oxford University Press, USA.

Eldredge, N., & Stanley, S. M. (1984). Living fossils: Introduction to the casebook. In *Living fossils* (pp. 1–3). Springer.

Enquist, M., Jansson, F., Ghirlanda, S., & Michaud, J. (2024). Cultural traits operating in senders are driving forces of cultural evolution. *Proceedings of the Royal Society B*, *291*(2018), 20232110.

Evans, A. R., Pollock, T. I., Cleuren, S. G., Parker, W. M., Richards, H. L., Garland, K. L., Fitzgerald, E. M., Wilson, T. E., Hocking, D. P., & Adams, J. W. (2021). A universal power law for modelling the growth and form of teeth, claws, horns, thorns, beaks, and shells. *BMC biology*, *19*, 1–14.

Gilbert, L. (2019). "assassin's creed reminds us that history is human experience": Students' senses of empathy while playing a narrative video game. *Theory & Research in Social Education*, *47*(1), 108–137.

Gould, S. J. (1974). The origin and function of 'bizarre' structures: Antler size and skull size in the 'irish elk,' megaloceros giganteus. *Evolution*, 191–220.

Gray, R. D., Greenhill, S. J., & Ross, R. M. (2007). The pleasures and perils of darwinizing culture (with phylogenies). *Biological Theory*, *2*, 360–375.

Henrich, J. (2016). *The secret of our success: How culture is driving human evolution, domesticating our species, and making us smarter*. Princeton University press.

Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and human behavior*, *22*(3), 165–196.

Hidalgo, C. A., Klinger, B., Barabási, A.-L., & Hausmann, R. (2007). The product space conditions the development of nations. *Science*, *317*(5837), 482–487.

Juul, J. (2011). *Half-real: Video games between real rules and fictional worlds*. MIT press.

Kauffman, S. (1969). Homeostasis and differentiation in random genetic control networks. *Nature*, *224*(5215), 177–178.

Ke, Q., Ferrara, E., Radicchi, F., & Flammini, A. (2015). Defining and identifying sleeping beauties in science. *Proceedings of the National Academy of Sciences*, *112*(24), 7426–7431.

Kent, S. L. (2010). *The ultimate history of video games, volume 1: From pong to pokemon and beyond... the story behind the craze that touched our lives and changed the world* (Vol. 1). Crown.

Kocurek, C. A. (2015). *Coin-operated Americans: Rebooting boyhood at the video game arcade*. U of Minnesota Press.

Koppl, R., Gatti, R. C., Devereaux, A., Fath, B. D., Herriot, J., Hordijk, W., Kauffman, S., Ulanowicz, R. E., & Valverde, S. (2023). *Explaining technology*. Cambridge University Press.

Lappo, E., Rosenberg, N. A., & Feldman, M. W. (2023). Cultural transmission of move choice in chess. *Proceedings of the Royal Society B*, *290*(2011), 20231634.

Liow, L. H., & Stenseth, N. C. (2007). The rise and fall of species: Implications for macroevolutionary and macroecological studies. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1626), 2745–2752.

Lloyd, G. T., Wang, S. C., & Brusatte, S. L. (2012). Identifying heterogeneity in rates of morphological evolution: Discrete character change in the evolution of lungfish (sarcopterygii; dipnoi). *Evolution*, *66*(2), 330–348.

Lowood, H. (2009). Videogames in computer space: The complex history of pong. *IEEE Annals of the History of Computing*, *31*(3), 5–19.

MAME. (2023). Multiple arcade machine emulator (MAME) project [Accessed: 2024-03-05]. https://www.mamedev.org Markoff, J. (1981). Atari acts in an attempt to scuttle software pirates. *InfoWorld*, 28–29.

McGhee, G. R. (1999). *Theoretical morphology: The concept and its applications*. Columbia University Press.

Mesoudi, A. (2011). *Cultural evolution: How darwinian theory can explain human culture and synthesize the social sciences*. University of Chicago Press.

Mesoudi, A. (2020). Cultural evolution of football tactics: Strategic social learning in managers' choice of formation. *Evolutionary Human Sciences*, *2*, e25.

Mesoudi, A., & O'Brien, M. J. (2008). The cultural transmission of great basin projectile-point technology i: An experimental simulation. *American Antiquity*, *73*(1), 3–28.

Montfort, N., & Bogost, I. (2009). *Racing the beam: The Atari video computer system*. Mit Press.

Newman, M. Z. (2018). *Atari age: The emergence of video games in america*. MIT Press.

Raessens, J., & Goldstein, J. (2011). *Handbook of computer game studies*. Mit Press.

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

Raulo, A., Rojas, A., Kröger, B., Laaksonen, A., Orta, C. L., Nurmio, S., Peltoniemi, M., Lahti, L., & Žliobaite, I. (2023) What are patterns of rise and decline? *Royal Society Open Science*, *10*(11), 230052.

Raup, D. M., & Michelson, A. (1965). Theoretical morphology of the coiled shell. *Science*, *147*(3663), 1294–1295.

Reali, F., & Griffiths, T. L. (2010). Words as alleles: Connecting language evolution with bayesian learners to models of genetic drift. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1680), 429–436.

Sobchuk, O., Youngblood, M., & Morin, O. (2024). First-mover advantage in music. *EPJ Data Science*, *13*(1), 37.

Solé, R., & Valverde, S. (2020). Evolving complexity: How tinkering shapes cells, software and ecological networks. *Philosophical Transactions of the Royal Society B*, *375*(1796), 20190325.

Solé, R. V., Valverde, S., Casals, M. R., Kauffman, S. A., Farmer, D., & Eldredge, N. (2013). The evolutionary ecology of technological innovations. *Complexity*, *18*(4), 15–27.

Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Blackwell Publishers.

Spiridonov, A., & Eldredge, N. (2024). The bretskyan hierarchy, multiscale allopatry, and geobiomes—on the nature of evolutionary things. *Paleobiology*, *50*(2), 194–213.

Stanley, S. M. (1975). A theory of evolution above the species level. *Proceedings of the National Academy of Sciences*, *72*(2), 646–650.

Strotz, L. C., & Lieberman, B. S. (2023). The end of the line: Competitive exclusion and the extinction of historical entities. *Royal Society Open Science*, *10*(2), 221210.

Tëmkin, I., & Eldredge, N. (2007). Phylogenetics and material cultural evolution. *Current anthropology*, *48*(1), 146–154.

Therrien, C. (2015). Inspecting video game historiography through critical lens: Etymology of the first-person shooter genre. *Game Studies*, *15*(2).

Todorov, T. (1975). *The fantastic: A structural approach to a literary genre* [Originally published in French as *Introduction à la littérature fantastique* (1970)]. Cornell University Press.

Turchin, P., & Gavrilets, S. (2021). Tempo and mode in cultural macroevolution. *Evolutionary Psychology*, *19*(4). https://doi.org/10.1177/14747049211066600

Valverde, S. (2021). The long and winding road: Accidents and tinkering in software standardization. *Mètode Science Studies Journal*, *11*, 91–97.

Valverde, S., & Solé, R. V. (2006). On the nature of design. In *Complex engineered systems: Science meets technology* (pp. 72–100). Springer.

Valverde, S., & Solé, R. V. (2015). Punctuated equilibrium in the large-scale evolution of programming languages. *Journal of The Royal Society Interface*, *12*(107), 20150249.

Vidiella, B., Carrignon, S., Bentley, R. A., O'Brien, M. J., & Valverde, S. (2022). A cultural evolutionary theory that explains both gradual and punctuated change. *Journal of the Royal Society Interface*, *19*(196), 20220570.

Vrba, E. S., & Eldredge, N. (1984). Individuals, hierarchies and processes: Towards a more complete evolutionary theory. *Paleobiology*, *10*(2), 146–171.

West, G. B., Brown, J. H., & Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, *276*(5309), 122–126. https://doi.org/10.1126/science.276.5309.122

Wolf, M. J. (2012). Battlezone and the origins of first-person shooting games. *Guns, Grenades, and Grunts*, 25.

Zhang, H., & Mace, R. (2021). Cultural extinction in evolutionary perspective. *Evolutionary Human Sciences*, *3*, e30.

Žliobaite, I., Fortelius, M., & Stenseth, N. C. (2017). Reconciling taxon senescence with the red queen's hypothesis. *Nature*, *552*(7683), 92–95.

Appendix A: Glossary of Key Terms

Term	Definition
Arcade Video Game	A coin-operated electronic game designed for short, replayable play sessions, typically housed in a dedicated cabinet.
Genre	A culturally constructed category of games defined by shared gameplay mechanics and aesthetics.
Subgenre	A finer classification within a genre that captures specialized features or themes.
Morphospace	A conceptual design space defined by CPU speed and ROM size, representing the multidimensional landscape of viable arcade system configurations. It is used to analyze technological and gameplay diversity across niches.
Scaling Law	A power-law relationship describing how one variable scales relative to

	another across arcade systems.
Allometry	Abiologicalscalingprincipleappliedheretoexplaingrowthpatternsinarcade hardware traits.
Trait	A measurable property of a system, specifically ROM size or CPU speed.
Trait Diversity ($V(N)$)	The number of unique trait combinations in a niche as a function of the number of games.
Scaling Exponent (a, b)	A power-law parameter quantifying how CPU or trait diversity scales with system size.
Imitation	The replication of existing game designs with minimal novelty.
Bootleg	An unauthorized clone of a game that reuses hardware or software without permission.
Collaboration	A licensed or joint development involving multiple firms that contributes to innovation.
Combinatorial Innovation	The generation of novelty through the reassembly of existing components—hardware traits, gameplay mechanics, or cultural practices—into new, functionally distinct configurations. Enabled by modularity and collaboration, it drives exploration of morphospace and supports niche resilience.
Dilution of Expertise Hypothesis	A model suggesting cultural collapse occurs when imitation exceeds innovation.
Niche Collapse	A decline in the diversity and viability of a niche—whether a genre or subgenre—due to saturation, imitation, or technological stagnation.
Recombination	The mixing of distinct traits—such as ROM and CPU configurations—within a niche or system lineage. Often observed indirectly through patterns of trait diversity, recombination reflects the capacity to explore design space by integrating variations, regardless of whether novelty is functionally transformative.
Resilience (of a niche)	A niche's ability to remain viable through innovation and adaptation.
Living Fossil (cultural)	A niche that persists with minimal innovation, akin to stasis in biological evolution.
Downward Causation	Influence exerted by niche-level constraints on individual game design.
Cultural Macroevolution	Large-scale, long-term changes in cultural systems involving diversification and extinction.

Appendix B: Arcade Video Game Dataset

The Multiple Arcade Machine Emulator (MAME) is an open-source project dedicated to preserving the history of arcade games by emulating a wide range of legacy hardware systems. Originally designed for accurate hardware emulation, MAME has evolved into a comprehensive public archive containing metadata on thousands of machines, including information on game titles, manufacturers, release years, hardware configurations, and gameplay genres (MAME, 2023). The dataset includes 7,205 unique game titles. However, because some games involved multiple firms (e.g., in licensing or regional distribution), the full dataset contains 7,822 firm–game entries. This reflects a bipartite network between developers and games, with each edge corresponding to a collaborative relationship. All diversity and scaling analyses are based on de-duplicated game entries unless stated otherwise.

To construct our arcade game dataset, we extracted game records from MAME's internal database by generating an XML dump of all available entries. This file can be created using the following command:

```
mame -listxml > database.xml
```

We developed a custom Python parser to process this file. For each game, we retrieved metadata such as title, manufacturer, release year, ROM size (bytes), and CPU clock speed (Hz). To facilitate evolutionary and macro-level analysis, these continuous variables were log-transformed. In parallel, genre information (main and sub-category) was obtained from external community-maintained classification files—specifically catver.ini and category.ini—which are periodically updated by MAME contributors and curatorial groups such as Arcade Italia and MAMEUI. These files reflect a retrospective, crowd-sourced consensus about genre classification, developed over decades of community curation and gameplay documentation. Our analysis focused on games belonging to seven core genres: *Arcade*, *Shooter*, *Platform*, *Fighter*, *Driving*, *Maze*, and *Ball & Paddle*. We excluded entries marked as "hack" to ensure that only officially released games contributed to our tree and diversity metrics.

These classifications are inherently historical rather than theoretical in nature. Following Todorov's distinction (Todorov, 1975), the genre categories used here are best understood as *historical genres*—emerging through retrospective interpretation and collective usage—rather than *theoretical genres* defined by formal gameplay rules or design taxonomies. The classification system embedded in MAME is the outcome of ongoing interactions among a heterogeneous community that includes players, arcade historians, emulation software developers, and preservation practitioners. As such, these labels do not reflect a universal taxonomy established at the time of release, but rather a socially constructed, evolving scaffold that structures collective memory and supports systematic comparison across decades of arcade game development.

While we preserve the original main and sub-genre classifications from the community files without alteration, we introduce one analytical coarse-graining step to define the "Shooter / Aerial Combat" group, which combines six closely related subcategories. This grouping, used exclusively in Figures 7b and 7d to enhance the statistical fit of diversity curves, does not alter the underlying dataset and is defined explicitly in the source code as:

```
Aerial Combat IDs: {0, 14, 21, 26, 47, 52}
```

where the category id´s correspond to the Shooter subgenres "Flying" (0), "Flying Diagonal" (52), "Flying Vertical" (21), "Flying Horizontal" (26), "Flying 1st Person" (14) and "Flying (chase view)" (47).

We reconstruct a genre tree by interpreting the main and sub-genre labels as a branching structure that reflects the diversification of gameplay mechanics over time. While the XML file itself does not define this structure, we use the earliest known appearance of each subgenre to order the tree temporally. The resulting visualization (Figure 1) is not a genealogical tree in the biological sense, but a heuristic representation of gameplay differentiation, consistent with models of cultural and technological evolution. It allows us to analyze patterns of niche expansion, genre saturation, and the long-term persistence of arcade game forms.

Appendix C: Trait canalization in technological morphospaces

Innovation in cultural systems takes place within structured morphospaces where some directions are more accessible than others due to technological, economic, or historical constraints. In arcade video games, two key hardware traits—ROM size (M) and CPU speed (S)—co-evolved under a scaling law of the form $S \sim M^a$ (Equation 1). This empirical relationship, analogous to biological allometries, defines a constrained surface within the larger design space of possible arcade configurations.

At the same time, the observed diversity of these traits across games within a given niche scales with output volume. That is, the number of unique ROM values, $V_M(N)$, and unique CPU values, $V_S(N)$, both tend to follow power-law relationships of the form:

$$V_M(N) \sim N^{b_M}, \quad V_S(N) \sim N^{b_S}$$

where N is the number of games and $b_M, b_S \in [0,1]$ are scaling exponents that quantify the rate at which diversity in each trait accumulates. Low exponents (e.g., $b < 0.4$) indicate stagnation or repetition, while values closer to 1 reflect ongoing exploration and recombination. Figure 7 in the main text illustrates these dynamics across several arcade subgenres.

The interplay between the two scaling relations—one describing the geometric constraint $S \sim M^a$, the other capturing how each trait diversifies with N—reveals a deeper dynamic of constraint amplification. To see this, suppose ROM values diversify as $V_M(N) \sim N^{b_M}$, and CPU speed is determined entirely by ROM via the scaling law $S = kM^a$. Because this mapping is deterministic and monotonic, each distinct ROM value corresponds to a unique CPU value, implying $V_S(N) \sim V_M(N)$.

Taking logarithms of both sides of the scaling law, we obtain log S = log k + a log M, so the spread of CPU speeds is linearly proportional to the spread of ROM values, scaled by the exponent a. It follows that:

$$b_S \sim a \cdot b_M$$

This result implies a constraint on how rapidly CPU diversity can grow, given the pace of ROM diversification and the steepness of the scaling curve. In collapsing niches, where ROM diversification is slow ($b_M \ll 1$), even a relatively steep scaling exponent a cannot prevent trait space from becoming narrowly canalized.

We use “canalization” here in an extended sense: originally introduced in developmental biology and later formalized in complex systems theory (Kauffman, 1969), canalization describes how systemic constraints suppress sensitivity and guide trajectories toward stable or limited outcomes. In our context, it means that evolutionary trajectories through arcade morphospace—while technically improving—may become geometrically confined, with limited exploration across orthogonal trait dimensions. In other words, even as hardware performance grows, design diversity shrinks.

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press

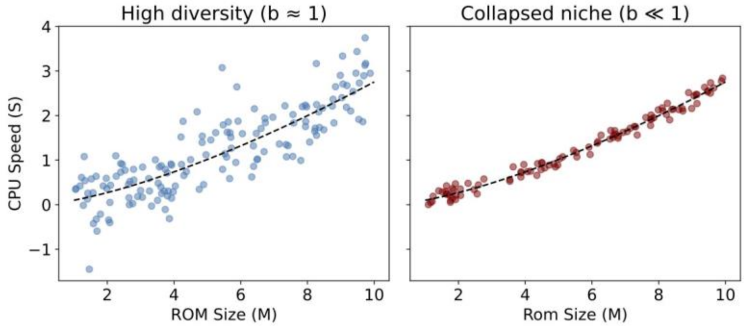

Figure 10. **Trait canalization in arcade morphospace**. Theoretical morphospace illustrating the effect of scaling constraints on niche trajectories. The dashed curve represents the scaling law $S \sim M^a$, defining the feasible region of hardware configurations (CPU speed vs. ROM size). In high-diversification regimes (left panel), niches explore a broad area around the scaling law. In collapsing niches (right panel), diversification slows and trajectories become canalized along the curve, exhibiting limited variation in either dimension. This narrowing reflects the effect of low b exponents on trait-specific diversity, consistent with the bound $b_S \sim a \cdot b_M$ (see text). In all panels $a = 1.44$.

Figure 10 illustrates how different diversification regimes map onto the structure of the arcade hardware space. High-diversity niches scatter broadly around the scaling curve, exploring both its trajectory and its neighborhood. Collapsing niches instead trace the curve tightly, with minimal variation. What may appear as steady technological progress can thus mask an underlying constraint in design possibilities

https://doi.org/10.1017/ehs.2025.10015 Published online by Cambridge University Press