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One Colony to Rule Them All: The Origins of Unicoloniality in Invasive Ants

Most ant species are committed to territorial defence where workers patrol boundaries, attack intruders, and protect their colony from neighbouring nests. But in the landscapes of California, the invasive Argentine ants break this rule entirely. Workers from nests hundreds of kilometres apart intermingle without aggression, forming what is effectively a single, borderless society (Tsutsui et al., 2000). This social structure – unicoloniality – emerges when territorial behaviour disappears across a population, allowing workers to move freely among physically separate nests. The result is the formation of immense supercolonies capable of stretching across thousands of kilometres (Giraud et al., 2002). At such scales, workers at opposite ends of the network will never meet, yet all behave as if they are members of the same colony.

Unicoloniality has major ecological consequences. Without the need to defend territorial borders, colonies can allocate more resources toward growth, enabling them to reach exceptionally high worker densities and dominate available resources (Holway, 1998). Yet, while unicoloniality remains relatively rare among ant species, it appears with an intriguing frequency among invasive species. Of the five ant species listed among the world's worst invaders, four exhibit unicolonial organisation (Lowe et al., 2001). Beyond Argentine ants (*Linepithema humile*), these include the little fire ant (*Wasmannia auropunctata*), the big-headed ant (*Pheidole megacephala*) and the crazy yellow ant (*Anoplolepis gracilipes*) – raising the question: why does unicoloniality appear so consistently in species that successfully invade new environments?

This review investigates how unicoloniality arises in introduced ant populations, arguing that it is best understood as the outcome of interacting genetic, behavioural, and ecological factors. The discussion traces research on founder effects and genetic bottlenecks to subsequent evidence that some species possess behavioural predispositions in their native ranges and, finally, to work showing how ecological conditions in introduced environments can further diminish aggression. By outlining these developments, the review provides an account of how different mechanisms play a role in the emergence of unicolonial social systems in invasive ants.

Early explanations for this phenomenon centred on founder effects – the loss of genetic diversity that occurs when a small number of individuals establishes a new population. When Tsutsui et al. (2000) compared Argentine ants in their native Argentine range to introduced Californian populations, they found dramatically reduced genetic diversity in the introduced range. Populations had lost approximately half their alleles and showed 68% lower genetic variation overall. This genetic loss correlated with behavioural changes. In Argentina, workers from neighbouring nests only metres apart frequently fought, whereas in California, even workers from nests separated by hundreds of kilometres showed no aggression whatsoever.

The link between genetic diversity and aggression lies in how ants recognise nestmates. Ants identify colony members by detecting cuticular hydrocarbons (CHCs) – long-chain waxy compounds on the surface of their exoskeletons that serve as chemical signatures (Tsutsui et al., 2000). These CHC profiles are influenced by genetics, and ants learn the odour template of their colony during development. In native populations with high genetic diversity, colonies produce diverse CHC profiles, allowing workers to distinguish between nestmates and non-nestmates. Ants set a threshold for how similar another ant must smell before it is accepted as part of the colony (Tsutsui et al., 2000). However, founder effects disrupt this system. When only a few individuals establish a new population, reduced genetic variation homogenises CHC profiles across the introduced population. Ants from different nests therefore smell almost identical – easily surpassing the acceptance threshold (Tsutsui et al., 2000). Although workers retain the ability to detect chemical differences, those differences are so slight that virtually no individual is recognised as foreign. Without aggression to enforce colony boundaries, nests that would normally be separate colonies behave cooperatively. As these cooperative networks expand across the landscape, they form the vast supercolonies characteristic of invasive populations.

Other invasive species show similar patterns. The tawny crazy ant (*Nylanderia fulva*) lost 60% of its genetic diversity during invasion of the United States – its allele count dropped from 153 in native South American populations to just 61 in introduced populations (Eyer et al., 2018). This genetic bottleneck coincided with a shift from multicolonial organisation in the native range, where genetic differentiation among nests accounted for 25.9% of total variation, to a unicolonial system in the introduced range, where genetic differentiation among nests was effectively zero (Eyer et al., 2018). Similarly, the little fire ant (*Wasmannia auropunctata*) in introduced New Caledonian populations exhibited uniformity in CHC profiles alongside reduced genetic diversity (Errard et al., 2005). The big-headed ant (*Pheidole megacephala*) also showed evidence of founder effects in Australian populations, where reduced genetic variation was associated with the formation of a supercolony extending over 3000 kilometres (Fournier et al., 2009).

However, founder effects alone cannot explain all cases of unicoloniality in introduced populations. Giraud et al. (2002) found that European Argentine ant populations experienced only a relatively mild genetic bottleneck. Simulations suggested that 18-39 founders would have been sufficient to generate the observed levels of genetic diversity, far more than expected if a severe loss of variation were responsible for the breakdown of nestmate recognition. This indicates that factors beyond simple genetic homogenisation must contribute to the emergence of unicoloniality.

Evidence from native-range populations further challenges a purely bottleneck-based explanation. Pedersen et al. (2006) found that Argentine ants in their native range already formed supercolonies with near-zero relatedness among nestmates. Within these native supercolonies, workers tolerated one another, while workers from different supercolonies remained highly aggressive. The main distinction between native and introduced populations was scale. Native supercolonies spanned only tens to hundreds of metres, whereas introduced supercolonies can extend thousands of kilometres. Similarly, big-headed ants (*Pheidole megacephala*) exhibit extensive unicoloniality in Australia, yet Fournier et al. (2012) documented supercolonial organisation in native Cameroon populations, though at smaller scales. Together, these findings suggest that unicoloniality is not necessarily a novel trait that arises only after introduction, pointing to a different explanation for the prevalence of unicoloniality among invasive species.

The discovery that some species form supercolonies even within their native ranges suggests that certain ants may be intrinsically predisposed toward this social structure. A clear example comes from comparisons between the invasive garden ant (*Lasius neglectus*) and its non-invasive sister species *Lasius turcicus*. When Cremer et al. (2008) studied both species in their shared native range, they found notable differences in their recognition systems despite their similar ecological settings.

The primary distinction lay in their cuticular hydrocarbon composition. *L. neglectus* workers produced CHC profiles dominated by long-chain hydrocarbons, whereas *L. turcicus* relied primarily on more volatile short-chain compounds (Cremer et al., 2008). Long-chain hydrocarbons evaporate slowly and generate weaker, less useful odour cues. As a result, even populations with comparable genetic diversity showed far lower chemical dissimilarity between nests in *L. neglectus* than in *L. turcicus*. This reduced chemical variation existed entirely within the native range – well before any introduction events – indicating that *L. neglectus* had evolved a recognition system inherently less capable of enforcing clear colony boundaries.

Cremer et al. (2008) proposed that supercolony formation in *L. neglectus* may have arisen through a multi-step evolutionary sequence in the native range, beginning with shifts in mating system and colony structure and later involving transitions toward less volatile recognition cues. This suggests that in some species, the capacity for unicoloniality is not a derived consequence of invasion but an intrinsic feature of their chemical and social biology.

At the same time, Cremer et al. (2008) also found that introduced *L. neglectus* populations had largely escaped their native parasites, indicating that these predispositions do not act alone. Instead, they interact with ecological conditions in the introduced range to enable the vast, persistent supercolonies characteristic of invasive populations. The same combination of pre-existing traits and favourable ecological circumstances likely underlies the expansion of smaller native supercolonies – such as those of the aforementioned Argentine ants and big-headed ants – into the enormous, landscape-spanning supercolonies seen in their introduced ranges.

What ecological conditions in introduced environments might amplify these existing predispositions? One factor appears to be nest density. Invasive ant populations often reach far higher densities than their native counterparts as they are freed from natural enemies like parasites and competitors, allowing nests to proliferate rapidly across invaded landscapes (Giraud et al., 2002). This density creates strong selection pressures against aggression.

High nest density affects unicoloniality in two ways. First, frequent encounters between neighbouring nests make territorial defence increasingly costly, as workers expend resources fighting and risk injury, with the costs potentially outweighing benefits. Second, colonies that avoid these conflicts gain a decisive advantage. Experimental studies demonstrated that Argentine ant colonies with non-aggressive neighbours achieved higher worker numbers than those constantly engaged in territorial battles (Giraud et al., 2002). In dense populations, peaceful colonies simply outgrow aggressive ones.

Under these conditions, colonies with chemically similar recognition cues encounter each other frequently but rarely fight. These colonies expand while aggressive colonies with distinctive chemical profiles waste resources on conflict. Over time, natural selection favours ants carrying common recognition variants while eliminating rare ones – a process Giraud et al. (2002) termed "genetic cleansing." Crucially, this differs from founder effects. Rather than random loss of alleles, active selection drives the change. European Argentine ant populations illustrated this clearly. Despite retaining substantial genetic diversity overall, aggression between nests depended entirely on supercolony membership rather than genetic similarity, indicating that selection had favoured particular recognition alleles independent of other genetic variation (Giraud et al., 2002).

Ecological conditions can also select directly against aggressive behavior itself, even when recognition abilities remain intact. The ant *Lasius austriacus* maintained clear discrimination between nestmates and non-nestmates yet showed no aggression between colonies (Steiner et al., 2007). When resources are abundant and competition limited – conditions typical of many introduced ranges – the costs of fighting may simply outweigh any benefits, making peaceful coexistence advantageous regardless of whether ants can distinguish colony membership. The combination of high nest densities selecting against rare recognition alleles and resource-rich environments making aggression unprofitable may explain why unicoloniality emerges so frequently in invasive ant populations. Moreover, this ecological pathway to reduced aggression has broader implications: if the right environmental conditions can promote supercoloniality even in species with intact recognition systems, then many more ant species than currently recognised as potential invaders might in fact possess the capacity to become invasive when introduced to appropriate habitats (Steiner et al., 2007).

The emergence of unicoloniality in invasive ant populations represents a remarkable convergence of chance, predisposition, and opportunity. Rather than arising from a single mechanism, the vast supercolonies that characterise these invasions result from the interplay of genetic accidents, evolutionary history, and ecological circumstance. Founder effects strip away genetic diversity, homogenising the chemical signatures that would otherwise define colony boundaries (Tsutsui et al., 2000; Eyer et al., 2018). Yet this loss alone cannot account for all cases – some invasive populations retain substantial genetic variation while still forming enormous supercolonies (Giraud et al., 2002). The missing piece lies in recognising that certain species arrive in new territories already equipped with chemical recognition systems predisposed toward weak colony boundaries (Cremer et al., 2008; Pedersen et al., 2006). These pre-existing traits interact with the ecological conditions of introduced environments – high nest densities and reduced competition – to amplify what were once modest supercolonies into landscape-dominating networks (Giraud et al., 2002; Steiner et al., 2007).

Understanding unicoloniality as the outcome of interacting genetic, behavioural, and ecological mechanisms has important implications for predicting invasions. When genetic quirks, pre-adapted recognition systems, and favourable ecological conditions converge, modest colonies can escalate into sprawling supercolonies, moving and foraging with seamless coordination. At this scale, the ecological impact can be devastating: entire landscapes can be transformed, native species displaced, and ecosystems destabilised. In the end, what begins as scattered colonies can coalesce into a single, dominant force – one colony to rule us all.

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