found by Knapp *et al.* and Sork *et al.*, studying oaks that usually grow in relatively low-density, savanna situations, might differ considerably from results from other species that grow in denser landscapes.

The good news is that such contrasting results give excellent indications of the potential for a rousing controversy over the role of pollen limitation and limited pollen dispersal in shaping the genetic structure and reproductive ecology of wind-pollinated trees. The answer might be in the wind but, with increasingly powerful molecular and analytical techniques combined with sophisticated models, the time is coming when we will be able to do more than just watch as it blows on by.

References
1 Knapp, E.E. *et al.* (2001) Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* 128, 48–55
2 Sork, V.L. *et al.* (2002) Pollen movement in declining populations of California valley oak, *Quercus lobata*: where have all the fathers gone? *Mol. Ecol.* 11, 1657–1668
3 Satake, A. and Iwasa, Y. (2002) Spatially limited pollen exchange and a long-range synchronization of trees. *Ecology* 83, 993–1005
4 Satake, A. and Iwasa, Y. (2002) The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. *J. Ecol.* 90, 830–838
5 Smouse, P.E. *et al.* (2001) Two-generation analysis of pollen flow across a landscape. I. Male gamete heterogeneity among females. *Evolution* 55, 260–271
6 Austerlitz, F. and Smouse, P.E. (2001) Two-generation analysis of pollen flow across a landscape. II. Relation between ϕ_{ft}, pollen dispersal, and inter-female distance. *Genetics* 157, 851–857
7 Austerlitz, F. and Smouse, P.E. (2001) Two-generation analysis of pollen flow across a landscape. III. Impact of within-population structure. *Genet. Res.* 78, 271–278
8 Vander Wall, S.B. (1990) *Food Hoarding in Animals*, University of Chicago Press
9 Satake, A. and Iwasa, Y. (2000) Pollen coupling of forest trees: forming synchronized and periodic reproduction out of chaos. *J. Theor. Biol.* 203, 63–84
10 Isagi, Y. *et al.* (1997) How does masting happen and synchronize? *J. Theor. Biol.* 187, 231–239
11 Ranta, E. *et al.* (1997) The Moran effect and synchrony in population dynamics. *Oikos* 78, 136–142
12 Larson, B.M.H. and Barrett, S.C.H. (2000) A comparative analysis of pollen limitation in flowering plants. *Biol. J. Linnean Soc.* 69, 503–520
13 Janzen, D.H. (1971) Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2, 465–492
14 Kelly, D. and Sork, V.L. (2002) Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* 33, 427–447
15 Smith, C.C. *et al.* (1990) The advantage of mast years for wind pollination. *Am. Nat.* 136, 1795–1807
16 Dow, B.D. and Ashley, M.V. (1998) High levels of gene flow in bur oak revealed by paternity analysis using microsatellites. *J. Hered.* 89, 62–70
17 Streiff, R. *et al.* (1999) Pollen dispersal inferred from paternity analysis in a mixed oak stand of *Quercus rober* L. and *Q. petraea* (Matt.) Liebl. *Mol. Ecol.* 8, 831–841
18 Dow, B.D. and Ashley, M.V. (1996) Microsatellite analysis of seed dispersal and parentage of saplings in bur oak, *Quercus macrocarpa*. *Mol. Ecol.* 5, 120–132
19 Berg, E.E. and Hamrick, J.L. (1995) Fine-scale genetic structure of a turkey oak forest. *Evolution* 49, 110–120
20 Sork, V.L. *et al.* (1993) Macrogeographic and fine-scale genetic structure in a North American oak species, *Quercus rubra* L. *Ann. Sci. For.* 50, 261s–270s
21 Schnabel, A. and Hamrick, J.L. (1990) Comparative analysis of population genetic structure in *Quercus macrocarpa* and *Q. gambelii* (Fagaceae). *Syst. Bot.* 15, 1
22 Kumar, A. and Rogstad, S.H. (1998) A hierarchical analysis of minisatellite DNA diversity in Gambel oak (*Quercus gambelii* Nutt Fagaceae). *Mol. Ecol.* 7, 859–869
23 Sork, V.L. *et al.* (1999) Landscape approaches to historical and contemporary gene flow in plants. *Trends. Ecol. Evol.* 14, 219–224
24 Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends. Ecol. Evol.* 9, 465–470
25 Koenig, W.D. and Knops, J.M.H. (1998) Scale of mast-seeding and tree-ring growth. *Nature* 396, 225–226
26 Curran, L.M. and Webb, C.O. (2000) Experimental tests of the spatio-temporal scale of seed predation in mast-fruiting dipterocarpaceae. *Ecol. Monogr.* 77, 129–148
27 Ostfeld, R.S. and Keesing, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends. Ecol. Evol.* 15, 232–237
28 Elkinton, J.S. *et al.* (1996) Interactions among gypsy moths, white-footed mice, and acorns. *Ecology* 77, 2332–2342
29 McShea, W.J. (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* 1, 228–238
30 Bolsinger, C.L. (1988) *The Hardwoods of California's Timberlands, Woodlands and Savannas*, USDA Forest Service, Pacific Northwest Research Station, Resource Bulletin PNW-RB-148
31 Standiford, R.B. (2002) California's oak woodlands. In *Oak Forest Ecosystems* (McShea, W.J. and Healy, W.M., eds) pp. 280–303, The Johns Hopkins University Press
32 Stahle, D.W. (2002) The unsung ancients. *Nat. Hist.* 111, 48–53
33 Mensing, S. (1992) The impact of European settlement on blue oak (*Quercus douglasii*) regeneration and recruitment in the Tehachapi Mountains, California. *Madroño* 39, 36–46

Selection for uniformity: xenophobia and invasion success

Philip T. Starks

Department of Biology, Tufts University, Medford, MA 02155-5555, USA

One reason why ants fascinate us is the seemingly bipolar nature of their social interactions: harmonious cooperation within, and extreme aggression across, colonies. Recent work by Giraud and colleagues and by Tsutsui and colleagues explores a behavioral outlier in this dichotomy, the invasive Argentine ant *Linepithema humile*. Introduced *L. humile* often form unicolonial societies in which conflict between colonies is absent.

Corresponding author: Philip T. Starks (philip.starks@tufts.edu).

Using theoretical, laboratory and field-based research, these researchers address an evolutionary paradox: the evolution of indiscriminate altruism.

Ants are among the most dominant animals on Earth [1]. One key to their superiority is their social system. Most ants are eusocial, meaning that they live in multi-generational groups, provide cooperative care for the young, and have a reproductive division of labor [1]. Although a common social system, the evolution of eusociality remained a mystery during the century between Darwin [2] and Hamilton [3] because theoreticians did not examine the question from a genetic perspective. Hamilton did, of course, as his resultant inequality – commonly referred to as Hamilton's rule – incorporated relatedness between individuals with the respective costs and benefits of a behavior and indicated when an altruistic act would be selectively advantageous [3]. Predictably, Hamilton's 'kin selection' insight resulted in a flood of kin recognition experiments (reviewed in [4−6]). In an interesting turn of events, Giraud and colleagues [7] and Tsutsui and colleagues [8] now use theory and methods common to recognition system research to describe a theoretical paradox: the evolution of indiscriminate altruism in the Argentine ant *Linepithema humile*.

Linepithema humile is among the most successful invasive species [9]. In at least two areas (California and Southern Europe), the introduced population has gone through a significant change in its social behavior [7,8,10,11]. Although more tolerant of non-nestmates than are most species of ants, native Argentine ants typically react aggressively toward conspecifics that come from nests more than a kilometer away. However, these invasive populations treat almost any conspecific as a nestmate, thus obliterating all colony boundaries. This form of social system is called unicoloniality [1] and, although it can increase invasion success [12], indiscriminate altruism is a bit of an evolutionary enigma. In two new papers, Giraud and colleagues [7] and Tsutsui and colleagues [8] make use of these invasive populations as natural experiments and present independent models of the evolution of unicoloniality.

Love thy neighbor, but only away from home
Giraud and colleagues [7] focus on the European *L. humile* introduced population. Although calculated differently, genetic analyses suggest that this introduced population did not experience as severe a genetic bottleneck as the Californian *L. humile* introduced population (28% and 57% reduction in allelic diversity, respectively; see [7,10,11]). Neutral arena behavioral studies of 1151 pairs of field-captured animals confirm previously published results: *Linepithema humile* show no aggression toward local conspecifics, regardless of nestmate status, but show extreme aggression toward conspecifics from other unicolonial populations. These results are sufficiently consistent, and the behavior sufficiently bipolar, to enable Giraud and colleagues to identify two unicolonial populations, one of which ranges over 6000 km and which

might qualify as the largest cooperative unit ever identified.

Other than identifying an enormous cooperative unit, why is this information interesting? After all, other studies of invasive *L. humile* have shown this breakdown in normal nestmate discrimination behavior (see e.g. [13]). What is interesting here is that, unlike the Californian population, this European population does not appear to have experienced as extreme a genetic bottleneck upon introduction. Because the bottleneck is often a central component of the hypothesized route to the evolution of unicoloniality [10,11], Giraud and colleagues had to develop an alternative. They suggest a two-step route to unicoloniality. Invading populations were first released from ecological constraints, which led to high population densities. High densities resulted in an increased encounter rate between non-nestmates, which led to selection against individuals with diverse recognition loci. This latter step is suggested to result in the disassociation between the recognition loci and the neutral microsatellite loci used to determine population genetic diversity.

Because this suggestion cannot be directly tested without first identifying the recognition loci, and because it is central to the explanation, researchers will need to test this hypothesis indirectly by examining the genetic contribution to the cuticular hydrocarbons, the physical cues the ants are most likely to use in recognition. Comparing the European and Argentine *L. humile* ant populations and showing that the genetic-based hydrocarbon cues in the introduced population are significantly less variable relative to the population genetic structure than are those in the native population appears to be the next logical step in this research program.

Tsutsui and colleagues [8] focus on the Californian *L. humile* population and take the investigation of this population a few exciting steps further. Previously, they showed that the population underwent a severe genetic bottleneck when first introduced [10,11] and they suggest that this is the central reason for the lack of nestmate discrimination. Their argument is that the level of population genetic diversity correlated with the recognition loci diversity and, at very low levels of recognition loci diversity, the ants are unable to distinguish nestmates from non-nestmates. Giraud and colleagues' work supports this hypothesis, the primary difference being that one population started with low recognition loci diversity (Californian) and the other (European) arrived at that point through selection against recognition cue diversity. Tsutsui and colleagues also invoke selection against recognition loci diversity (an idea first promoted by Crozier [14]) and suggest that this mechanism functions to maintain the unicolonial structure of their population.

The truly admirable aspect of the study by Tsutsui and colleagues is that they managed to test so many of their hypotheses. Neutral arena behavioral studies of 607 pairs of field-captured animals not only showed the polarized aggression previously mentioned, but also showed the outcome of such behavior. It turns out that being the initiator of aggression in 'ant fights' is better, at least if the ant wants to survive. And who is the aggressor? The
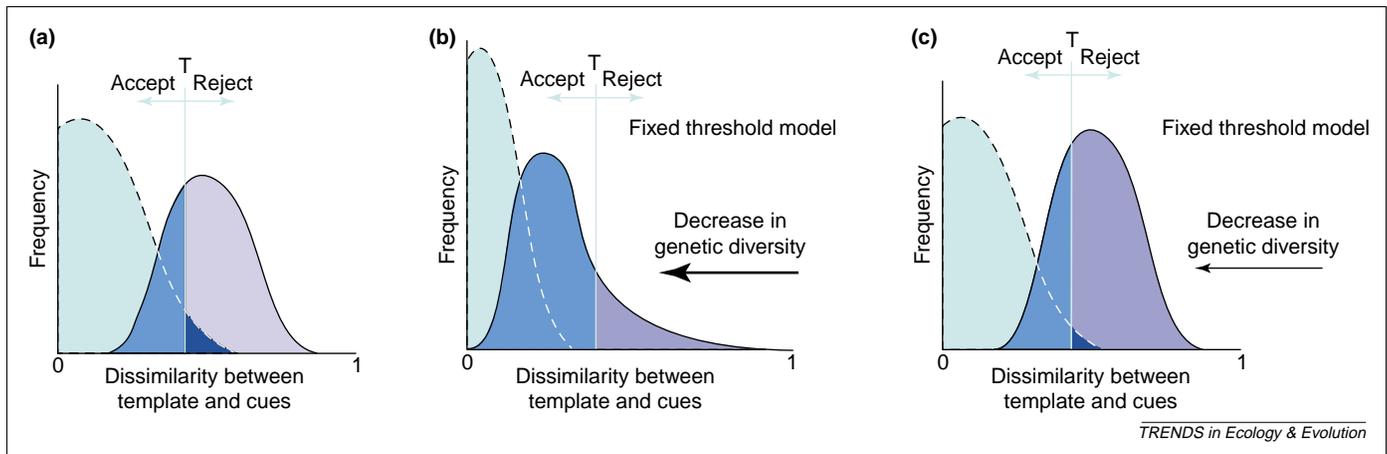
Fig. 1. Hypothetical frequency distributions of dissimilarity between an individual's recognition template and all possible conspecific recognition cues. Broad distributions of dissimilarity scores can occur when nestmate groups contain multiple genetic lines (see [28]) or when recognition cues incorporate environmental compounds, as is the case with Argentine ants [29]. Dissimilarity scores between nestmates will typically be lower than between non-nestmates. 'T' is the threshold above which individuals are rejected and below which individuals are accepted. In (a–c), dark blue areas indicate rejected nestmates and light-blue areas indicate accepted non-nestmates. (a) A native Argentine ant population in which non-nestmates are frequently discriminated against. Rejected non-nestmates in a multicolonial population are shown in light purple. (b) The invasive US Argentine ant population as hypothesized by Tsutsui and colleagues [8], in which non-nestmates frequently experience preferential treatment. Rejected non-nestmates, that is, those conspecifics that do not belong to a given unicolonial population (these individuals can be geographically distant from the unicolonial population) are shown in dark purple. The genetic bottleneck experienced upon invasion has shifted the dissimilarity distributions below the fixed acceptance threshold. (c) The invasive European Argentine ant population as hypothesized by Giraud and colleagues [7]. The coloration is used as in (b). The genetic bottleneck experienced upon invasion was small and has only slightly shifted the dissimilarity distributions. The frequency of interaction with non-nestmates increased post invasion leading to a disassociation between neutral genetic markers and recognition loci. Adapted, with permission, from [15].

aggressor – and probable survivor – is significantly more likely to be the ant that belongs to the less genetically diverse colony. Tsutsui and colleagues show this using behavioral assays and genetic analysis of an additional 124 pairs of ants, half of which (one ant from each pair) came from lab-maintained low genetic diversity colonies. Based on these data, Tsutsui and colleagues suggest a model for the evolution and maintenance of unicoloniality for the Californian *L. humile* introduced population: indiscriminate altruism as a result of genetic bottleneck followed by severe directional selection against genetic diversity, thus maintaining unicoloniality in the population. The mechanism here is not simply hypothesized; it is supported with empirical data.

The differences in the hypotheses for the evolution of unicoloniality presented here are relatively minor, and seem to reflect respective study systems rather than representing flaws in either group's interpretation. For the maintenance of unicoloniality, both hypothesized routes require selection against diversity, a factor that Tsutsui and colleagues clearly demonstrate is present within their system. The issue of the origin of the trait is thornier because it is notoriously difficult to infer the origins of a trait from its current utility. To discriminate between the hypotheses of the origin of unicoloniality, it is useful to visualize them within the framework of an acceptance threshold model [15].

Recognizing the similarities
Basic recognition system theory posits that individuals develop recognition templates, compare the cues of encountered conspecifics to this template, and decide whether the encountered individual is kin (or a nestmate) based on the degree of mismatch between the recognition template and the encountered individual's recognition cues (reviewed in [6]). This can be visualized using an

acceptance threshold model where a threshold based on template-cue dissimilarity is hypothesized to exist, above which conspecifics are rejected and below which they are accepted [15]. Assuming overlap between the dissimilarity distributions for kin and non-kin, recognition errors (i.e. rejection of kin and acceptance of non-kin) are unavoidable (Fig. 1a). The model by Tsutsui and colleagues can be considered a fixed threshold model where, owing to the severe genetic bottleneck the population experienced upon invasion, the dissimilarity index of local non-nestmates is below the acceptance threshold (Fig. 1b). As the population grew, the degree of dissimilarity was maintained below the acceptance threshold because of selection against diversity.

Giraud and colleagues also suggest a fixed threshold model, but hypothesize an initial stage when the population retained nestmate discrimination abilities, and as such was somewhat kin structured. As this population grew (Fig. 1c), costly interactions between non-nestmates increased in frequency, which led to selection against unique recognition loci and a disassociation between neutral and recognition loci. Over time, this disassociation resulted in a population that was genetically diverse at loci other than recognition loci, and this population coalesced into a unicolonial unit. Presumably, unicoloniality does not occur in the native range because some factor other than conspecific interactions places limits on population size. The acceptance threshold model (Fig. 1), used here to describe the hypothesized origins of unicoloniality in these invasive populations, makes explicit predictions regarding dissimilarity indices, and might enable these teams to make specific predictions regarding recognition cue variation in their populations and how the animals should respond to a given degree of cue dissimilarity (see e.g. [16]).

From one invasion to another

These teams have presented two views of the evolution of unicoloniality. Unicoloniality represents an extreme situation where individuals do not discriminate between nestmates and non-nestmates [1], and is rare (although less so among invasive ants [17]). Decreased interspecific competition after introduction, however, might not be rare, and release from conspecific pressures could enhance invasion success. Future research of non-native species should follow the methods of the Tsutsui team and examine the behavior of the animal in both its native and non-native territories. For example, the paper wasp *Polistes dominulus* is an extremely successful non-native animal in the USA [18]. Recent evidence indicates that at least part of its success can be attributed to high colony productivities [19,20] and its willingness to colonize previously unused territories [21]. Although *P. dominulus* discriminates nestmates from non-nestmates in both its native [22] and non-native [23,24] territories, it is not yet known if the degree of discrimination differs between native and introduced populations, and if any difference in conspecific interactions influences invasion success.

Initial population establishment and eventual invasion success are, of course, of primary interest to conservation biologists. Whether the potentially novel behavior of the invasion population remains unchanged is a different question, and one that is of utmost interest to evolutionary biologists [see 25]. Although using evolution-based models, neither Giraud and colleagues nor Tsutsui and colleagues discuss the long-term stability of unicolonialism in Argentine ants, and there is the push: these invasive ants – as dominant in their new territories as they are – could be living in an evolutionarily unstable social system, doomed to degenerate back to a state of intraspecific conflict [26]. Both research teams believe that unicoloniality is a temporary function of an expansion into a novel environment. As such, this research conveys a clear, but unspoken, message: evolution-based behavioral models and associated tests remain informative even when used on organisms that are no longer in the environment in which they evolved. Indeed, this is exactly why evolution-based animal behavior research in general, and recognition system research in particular, could revolutionize the field of invasion biology [27].

References

1 Hölldobler, B. and Wilson, E.O. (1990) *The Ants*, Harvard University Press
2 Darwin, C. (1859) *On the Origin of Species* (facsimile of 1st edn), Harvard University Press
3 Hamilton, W.D. (1964) The genetical evolution of social behaviour. I&II. *J. Theor. Biol.* 7, 1–52
4 Fletcher, D.J.C., Michener, C.D. eds (1987) *Kin Recognition in Animals* John Wiley and Sons
5 Hepper, P.G. ed. (1991) *Kin Recognition* Cambridge University Press
6 Sherman, P.W. *et al.* (1997) Recognition systems. In *Behavioural Ecology*, 4th edn, (Krebs, J.R. and Davies, N.B., eds) pp. 69–96, Blackwell Science
7 Giraud, T. *et al.* (2002) Evolution of supercolonies: the Argentine ants of southern Europe. *Proc. Natl. Acad. Sci. U. S. A.* 99, 6075–6079
8 Tsutsui, N.D. *et al.* Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. *Proc. Natl. Acad. Sci. U. S. A.* (in press)
9 Suarez, A.V. *et al.* (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proc. Natl. Acad. Sci. U. S. A.* 98, 1095–1100
10 Tsutsui, N.D. *et al.* (2000) Reduced genetic variation and the success of an invasive species. *Proc. Natl. Acad. Sci. U. S. A.* 97, 5948–5953
11 Tsutsui, N.D. and Case, T.J. (2001) Population genetics and colony structure of the argentine ant (*Linepithema humile*) in its native and introduced ranges. *Evolution* 55, 976–985
12 Holway, D.A. *et al.* (1998) Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* 282, 949–952
13 Newell, W. and Barber, T.C. (1913) *The Argentine Ant*, USDA Bureau of Entomology Bulletin Number 122
14 Crozier, R.H. (1986) Genetic clonal recognition abilities in marine-invertebrates must be maintained by selection for something else. *Evolution* 40, 1100–1101
15 Reeve, H.K. (1989) The evolution of conspecific acceptance thresholds. *Am. Nat.* 133, 407–435
16 Suarez, A.V. *et al.* (2002) Spatiotemporal patterns of intraspecific aggression in the invasive Argentine ant. *Anim. Behav.* 64, 697–708
17 Holway, D.A. *et al.* (2002) The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33, 181–233
18 Cervo, R. *et al.* (2002) *Polistes dominulus* (Hymenoptera Vespidae) invading North America: some hypotheses for its rapid spread. *Insect. Soc.* 47, 155–157
19 Pickett, K.M. and Wenzel, J.W. (2000) High productivity in haplo-metrotic colonies of the introduced paper wasp *Polistes dominulus* (Hymenoptera: Vespidae; Polistinae). *J. New York Entomol. Soc.* 108, 314–325
20 Gamboa, G.J. *et al.* (2002) The comparative biology of two sympatric paper wasps, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). *Insect. Soc.* 49, 45–49
21 Starks, P.T. Natal nest discrimination in the paper wasp, *Polistes dominulus*. *Ann. Zool. Fenn.* (in press)
22 Dani, F.R. *et al.* (1996) Behavioural evidence for the involvement of Dufour's gland secretion in nestmate recognition in the social wasp *Polistes dominulus* (Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.* 38, 311–319
23 Starks, P.T. *et al.* (1998) Context-dependent nestmate discrimination in the paper wasp, *Polistes dominulus*: a critical test of the optimal acceptance threshold model. *Anim. Behav.* 56, 449–458
24 Pickett, K.M. *et al.* (2000) Nestmate recognition in the absence of a pheromone. *Insect. Soc.* 47, 212–219
25 Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends Ecol. Evol.* 17, 386–391
26 Queller, D.C. and Strassmann, J.E. (1998) Kin selection and social insects. *Bioscience* 48, 165–175
27 Holway, D.A. and Suarez, A.V. (1999) Animal behavior: an essential component of invasion biology. *Trends Ecol. Evol.* 14, 328–330
28 Starks, P.T. *et al.* (1998) The effect of queen number on nestmate discrimination in the facultatively polygynous ant *Pseudomyrmex pallidus* (Hymenoptera: Formicidae). *Ethology* 104, 573–584
29 Chen, J.S.C. and Nonacs, P. (2000) Nestmate recognition and intraspecific aggression based on environmental cues in Argentine ants (Hymenoptera: formicidae). *Ann. Entomol. Soc. Am.* 93, 1333–1337