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Ilkka Hanski: The legacy of a multifaceted ecologist

Ilkka Hanski, The "Compleat Ecologist": an homage to his contributions to the spatial dimension of food web interactions

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Ilkka Hanski is most widely known for his seminal contributions to metapopulation ecology, both theoretical and empirical. But he also made many important and wide-ranging contributions to other arenas of ecological inquiry, including in particular predator–prey, host–parasitoid, and host–pathogen interactions. This paper provides an overview of his work in trophic ecology, ranging from individual behavior of foraging predators and fleeing prey, up to effects of spatial patchiness on the persistence of specialist natural enemies, and even the determinants of food chain length. In recent years, his work on food web interactions took on an increasingly genetic and evolutionary slant. In this paper, I also return to two theoretical models that I discussed over the years with Ilkka, where we contemplated carrying out collaborative work, but never managed to do so. The first of these models involves how habitat patchiness might moderate apparent competition between prey species. The second of these has to do with splicing evolutionary dynamics into metapopulation models, so as to craft hypotheses about how food chain length might be influenced by the coevolutionary struggle between predators and their prey. I developed simple models of the sort we should have explored together, in the style we would have used at the time of our conversations on these themes, in homage to my memory of our interactions.

Introduction

Ilkka Hanski to many scientists was "Dr. Metapopulation." In his long and highly distinguished career, Ilkka championed the critical role of spatial structure and dynamics for understanding population dynamics and persistence, not least in the context of landscapes radically altered by human activities, and with a particular focus on insect populations, such as the famed Glanville fritillary. Indeed, in the preface to his valedictory missive to the world, *Messages from Islands: A Global Biodiversity Tour* (Hanski 2016), he recounts how his love of biodiversity began with moth and butterfly chasing at the age of eight, and was sustained in particular by his capture in 1964 of a dusky meadow brown butterfly (*Hyponephele lycaon*), which had been thought to be extinct in Finland for some decades at the time. He never lost his interest in issues such as population rarity and extinction, and his professional career in some ways was an unfolding of a chrysalis of sustained intellectual orientations, developing out of his youthful enthusiasm for understanding diversity.

I suggest that we should also applaud Ilkka Hanski for his contributions well beyond metapopulation biology, for he was in many ways "The Compleat Ecologist" (with due acknowledgement to Izaak Walton 1653). Ilkka made significant contributions across all levels of ecological inquiry, ranging from early work on ecosystem processes in bogs (Silvola & Hanski 1979), through addressing broad-scale questions in biodiversity science (Hanski 1982, Rybicki & Hanski 2013), down to scrutinizing the level of behavioral ecology (e.g., Niitepõld *et al.* 2011) and even the microbiome of individual organisms (Hanski *et al.* 2012, Hanski 2014). His central abiding focus, however, was surely population biology, largely though not entirely in a spatial context, with an increasing emphasis on genetics and evolution in the latter part of his life (e.g., Fountain *et al.* 2016). In addition to hundreds of papers on population biology, Ilkka wrote or edited major books with a strong population focus (Gilpin & Hanski 1991, Hanski & Gilpin 1997, Hanski 1999, Hanski & Gaggiotti 2004). It is hard to imagine any corner of population and spatial ecology and conservation biology today that has not been influenced by his profound insights into how populations respond to spatial heterogeneity and patchiness in the environment.

Yet, throughout his career, Ilkka never lost sight of the importance of embedding an understanding of the population and evolutionary dynamics of each individual species into the broader context of the web of species in which it occurred. Many of his early papers focused on competitive interactions among species occupying naturally patchy environments, such as guilds of carrion flies (Hanski & Kuusela 1977) and dung beetles (Koskela & Hanski 1977, Hanski & Koskela 1979). These are all groups of species that can be viewed as classic competitors, in that they are similar species contending for similar resources, leading to the expectation of competitive interactions due to scramble competition and interference while contending for limited resources. But as Ilkka recognized, such competitive interactions emerge in part from trophic interactions, namely consumption of a shared, depletable resource base. Moreover, the patchiness and ephemeral nature of the resource base for these guilds, along with the intertwined vicissitudes of colonization, extinction, and local dynamics, could at times help facilitate competitive coexistence (Hanski 1983a). Understanding competitive coexistence is essential to elucidating controls on diversity on the "horizontal" dimension of communities. But communities also have a "vertical" structure of interlocked feeding interactions and other dependencies, sometimes expressed as simple food chains, and more often as complex webs of trophic interactions. Many horizontal interactions emerge from vertical interactions (as clearly recognized by Robert MacArthur in the early 1970s, in papers and monographs published about the time Ilkka Hanski was a student).

My paper is intended to pay homage to the many contributions that Ilkka Hanski made to our understanding of the vertical structure of ecological communities, ranging from the details of the trophic ecology of individual organisms, to predator–prey dynamics (and in particular the potential role of predation in driving rodent population cycles), to the consequences of trophic interactions for broader patterns of community structure and dynamics, to eco-evolutionary dynamics. In scanning his bibliography, I identified a substantial array of papers on these themes. By my count, Ilkka published 46 papers on trophic ecology, broadly conceived (and I have doubtless missed a few). This is a fine corpus of work, all on its own. Many of these contributions of course interdigitate with Ilkka's interest in spatial ecology, but not all.

Starting in the early 1980s, my path and Ilkka's intersected frequently, both in Finland and other venues, such as Imperial College at Silwood Park, and NCEAS in Santa Barbara. He kindly invited me to participate in a number of workshops in Finland, and to visit his lab at the University of Helsinki. We talked on many occasions about potential collaborations, and it is one of the great regrets of my life that we did not push these thoughts through to fruition. One thing I have done in thinking about what I might do in this homage to Ilkka is to go back through my notes and correspondence, and rummage in my memory, so as to allow some ideas to resurface. So I will attempt in this paper to provide a personal overview of some of the contributions Ilkka Hanski made over his life to the study of trophic interactions and food web ecology, and also to return to two specific thematic areas where he and I had thought to collaborate, but did not. I present some simple models illustrating — in a counterfactual world — what we might (and should) have done together, using the modeling approaches that would have occurred to us at the time we had those conversations. One of these has to do with how patchiness can modulate apparent competition, and the other with how evolutionary dynamics might influence food chain length. My intent for both of these is not to provide a comprehensive review of all the work that has subsequently emerged on these themes (though I will touch on that), but instead to provide homage to my friendship with Ilkka by developing thoughts that we never quite got around to publishing, using approaches that we would have used at the time.

The trophic ecology of individual organisms

At the most basic level, trophic ecology has to do with the struggle between consumers, trying to acquire resources, and their living resources, attempting to escape consumption. Until preparing this paper, I was unaware of (or had forgotten) several interesting empirical contributions Ilkka had made at this most basic level of trophic ecology.

For instance, he reported experiments (Hanski & Parviainen 1985) in which groups of pine sawfly cocoons (of the species *Nodiprion sertifer*) were placed at sites across a wide range of forest types, then monitored. These experiments showed that very rapid destruction of cocoons by small mammals occurred, suggesting that mammal predation could be a major driver of sawfly dynamics. The masked shrew was particularly effective in attacking spatially scattered cocoons, whereas the bank vole differentially hammered clumped cocoons. An intriguing detail parenthetically remarked on in the paper is that individual predators can retain memory of past locations of cocoon groups for a while, leading to spatially dependent predation. The paper ends by suggesting that these results may help explain the fact that sawfly outbreaks often start on barren soils, which have fewer generalist mammalian predators, permitting the inverse density dependence due to saturating functional responses by specialist predators to be particularly important in these populations.

There are several things that strike me about this paper. First, there is a concern with the spatial attributes of ecological systems. Second, there is a grounding of the population analyses in the details of organismal biology (how long can shrews and voles remember where they last encountered sawfly cocoons?). Finally, the authors aim to use local analyses to explain broader spatial patterns, such as the initial locations of sawfly outbreaks in heterogeneous landscapes. I think these themes resonate throughout a broad swathe of Ilkka's career.

Let me mention a couple of other contributions Ilkka made to individual trophic ecology. In Sundell *et al*. (2000), he reported experiments in which least weasels were given the opportunity to predate radio-collared *Microtus* voles, released into enclosures at different densities. Poor voles, they did not have a chance; over three days, a very large fraction of these prey were killed by the weasels. The weasels had a classic saturating, type II functional response, but with a killing rate greater than might be expected based just on the daily energetic demands of weasels. The bottom line of the study is that for *Microtus*, per capita mortality, though overall quite high, is reduced at higher conspecific densities. This basic relationship underlies many important ecological and evolutionary phenomena, ranging from explanations for population cycles, to the evolution of synchronized breeding, to group formation, and it is believed this contributes to the celebrated rodent outbreaks of Fennoscandian ecosystems (*see* below). A related paper (Hellstedt *et al*. 2002) showed that field vole movements, rate of maturation, and breeding success were not measurably altered by the simple presence of a key predator, the least weasel. This eliminates one potential source of complexity in population models of field voles impacted by predation. Peter Abrams (1984, 1995) among others (e.g., Kotler & Holt 1989) has long emphasized the particular importance of shifts in behavior and other traits as modulators of trophic interactions (what are now called "trait-mediated interactions," a growing field of interest in community ecology, Ohgushi *et al*. 2012). Peter gave a seminar in Helsinki in the early 1990s, visited with Ilkka (P. Abrams pers. comm.), and doubtless prompted Ilkka to think more carefully about the behavioral dimensions of trophic ecology. Studies such as Hellstedt *et al*. (2002) are important because they indicate that sometimes these potentially important complications may not be present in particular systems.

This concern with the details of the organismal dimension of trophic interactions continued in Ilkka's research right up to the present. For example, Duplouy *et al*. (2015) reported the impact of *Wolbachia* infection on a parasitoid (*Hyposoter horticola*, a specialist on the Glanville fritillary butterfly), and in particular on parasitoid fecundity and other direct fitness traits. The infection did not seem to affect these fitness traits of the host, but there *did* appear to be an influence on rates of hyperparasitism. This paper raises the fascinating possibility that infection by *Wohlbachia* could lead to a "bottom-up" trophic cascade, altering parasitoid-hyperparasitoid dynamics, thus in turn modulating impacts of the parasitoid on its butterfly host.

Predation and small mammal population dynamics

A more sustained dimension of Ilkka's research in trophic ecology was the population-level consequences of trophic interactions. In particular, he played a major role in championing the importance of predation for understanding rodent population dynamics in Fennoscandia, and by extension, elsewhere in the world. Ecologists have been intrigued by the causes of the oft-dramatic fluctuations in rodent population size since at least the 1920s (Elton 1924, Krebs 2013). Ilkka's initial interest in small mammal ecology was in shrew population dynamics (e.g., Kaikusalo & Hanski 1985), but in collaboration in particular with Lennart Hansson, Heikki Henttonen, and Peter Turchin, this shifted over time into a sustained and influential set of studies of microtine rodent dynamics. A landmark paper in 1991 (Hanski *et al*. 1991, cited according to Google Scholar over 600 times) argued that the relative importance of specialist and generalist predators varied systematically along a latitudinal gradient in Finland. Ilkka in this paper extended a predator–prey model explored by May (1973) (which in turn was based on Leslie 1948, and Leslie & Gower 1960) to examine the combined impacts of specialist and generalist predators on rodent cycles. The model is as follows:

$$dN/dt = rN(1 - N/K) - cPN/(N + D) - Gf(N),$$
$$dP/dt = sP[1 - P/(qN)].$$

Here N, P, and G are respectively the abundances of a focal prey population, a specialist predator upon it, and a generalist predator. The prey grows logistically on its own, but suffers mortality from both specialist and generalist predation. The specialist has a type II (saturating) functional response to the prey (which is key to facilitating outbreaks, and such a functional response indeed typifies the specialist mammalian predators of rodents, as shown in Sundell *et al*. 2000); the generalist was assumed to have an accelerating functional response to the focal prey, at least at low prey densities. The specialist predator dynamics phenomenologically follow a logistic growth equation, where predator carrying capacity is directly proportional to prey abundance. The number of generalist predators, G, is assumed fixed.

The model can produce predator and prey cycles, and it predicts that as generalist predator abundance increases, the magnitude of the oscillation decreases, as does the length of the prey cycle. At some point cycling entirely disappears, and a limit cycle is converted into a stable equilibrium. Both these predictions do match patterns observed in Fennoscandia, where cycle amplitude and period decline from north to south, and indeed cycling is not observed in southern latitudes.

These basic ideas were extended in a string of papers, impressive enough to be summarized in a separate paragraph in a *Proceedings of the National Academy of Sciences of the USA* encomium (Trivedi 2011). Hanski *et al.* (1994) responded to criticism by noting that comparable patterns emerge for other taxa (e.g., grouse) which are also affected by generalist predators, whose abundance and impacts vary systematically with latitude. Heikkilä *et al.* (1994) argued that regional synchrony of microtine rodent population dynamics was consistent with the role of a mobile, specialist predator, the stoat (*Mustela erminea*). With Peter Turchin, Ilkka (Turchin & Hanski 1997) showed that this model made quantitatively sensible predictions about latitudinal patterns in the amplitude and periodicity of population fluctuations. Follow-up papers (Turchin & Hanski 2001, Hanski *et al.* 2001) contrasted several alternative explanations, and concluded that the hypothesis of latitudinal shifts in the relative importance of specialist and generalist predators best fit the available evidence, compared to other plausible alternatives. Much of this work is synthesized in Turchin's monograph (Turchin 2003: 317–325). Sundell *et al.* (2004) reported that vole-eating avian predators have cyclic breeding success correlated with cyclic vole abundances, with latitudinal shifts in breeding success paralleling that of their rodent prey; they also show that vole cycles are spatially synchronized, in a way that matches dispersal abilities of their avian predators.

Ilkka also examined predation and rodent dynamics in another high latitude ecosystem — the high Arctic of Greenland. Gilg *et al.* (2003) examined in detail the collared lemming, and showed that the 40-year periodicity in lemming abundance observed in Greenland emerges robustly from time-lagged responses by a specialist predator (again the stoat), stabilized by direct density-dependent predation from several generalist predators (in this case, the arctic fox, the snowy owl, and the long-tailed jaeger). Gilg *et al.* (2009) revisited the theme of predator–prey cycles, in the context of climate change in the high Arctic. They conclude that climate change will likely reduce the reproductive success of predators, and might even lead to local extinctions. The model results match with the observed disappearance of lemming cycles in eastern Greenland in recent years. From the point of view of ecological theory, this paper utilized a different model formulation (as did Gilg *et al.* 2003) for the specialist predator than did earlier contributions by Ilkka on rodent dynamics, namely that stoat dynamics reflect a kind of classical Lotka-Volterra assumption, in that numerical responses of the specialist predator are related directly (albeit in a complicated way) to the abundance of its preferred prey, rather than following the logistic formulation of May (1973).

This is an impressive body of results. However, one potential weak link is that the population model explored in most of these papers assumes the Leslie-Gower predation model, in which the predator growth rate depends on the ratio of predator to prey abundances, rather than the rate of consumption of prey by predators. As has been noted (and questioned) by many authors (e.g., Arditi & Ginzburg 2012: 30; also P. Abrams pers. comm.), this assumption about logistic predator growth seems drawn from a hat, and may embody internal inconsistencies. The model is still being used at a fair clip by mathematical biologists doing purely theoretical studies (e.g., Gonzalez-Olivares *et al.* 2011, Gupta & Chandra 2013, Yue 2016), but the Leslie-Gower model has not been recently applied to empirical predator–prey systems, as best as I can tell. The main biological difficulty posed by the model formulation is that the numerical response of the predator does not really depend on the rate at which it is consuming the prey; if one fixes the predator/prey ratio, predator growth rate is fixed, even if the prey population goes to very low abundances where the functional response of the predator approaches zero. Gilg *et al.* (2003, 2009) abandoned this particular formulation, but still make assumptions about the coupling of numerical responses to functional responses that warrant more scrutiny. Future work on latitudinal gradients should explore different methods of linking predator functional and numerical responses by specialists and generalists as potential explanations for the latitudinal gradient in rodent oscillations. Traditional predator–prey models often neglect interference among predators that enters into the functional response, but such interference could well affect the magnitude of predator–prey cycles (and there is increasing evidence for interference among predators in functional responses, Abrams 2015).

To me, a major contribution of this body of work has been to emphasize the potential importance of the interplay of generalist and specialist predation in driving population fluctuations at high latitudes. Moreover, as noted by Krebs (2013), although these studies "do not suffice to conclusively demonstrate the validity of the predation hypothesis [for rodent population oscillations], the breadth of observations that can be resolved under it is impressive." The basic idea explored by Ilkka over several decades of thinking about small mammal population dynamics was that classic problems in population ecology might be best understood in the context of multispecies interactions in communities. This is a general insight that resonates well beyond the rodents of Fennoscandia, as well as beyond the limitations in the specific models explored by Ilkka and his colleagues.

Interspecific interactions in patchy and heterogeneous landscapes

Many of Ilkka's earliest scientific contributions were indeed in community ecology, for instance analyzing succession and niche relations in dung beetles (Koskela & Hanski 1977, Hanski & Koskela 1977). Ilkka's interest in community ecology continued throughout his career, with many intersecting research angles crucially involving spatial population dynamics. As one mark of this sustained interest, in each of the monographs and edited volumes noted above, there are one or more chapters dealing with multispecies interactions. In Hanski (1999), for example, chapter 7 deals with the interface between metapopulation and metacommunity theory. This included pairwise competition in a patchy environment, coexistence of predators and prey due to spatial dynamics surmounting local instability and predator-driven extinctions, and complex spatial patterns emerging in spatially explicit predator–prey and host–parasitoid interactions. Ilkka kindly invited me to contribute a chapter on fusing metapopulation and metacommunity perspectives in his 1997 edited volume (Holt 1997), and he later reciprocated by providing a lovely synthetic chapter in my own edited volume on metacommunity ecology (van Nouhuys & Hanski 2005). As van Nouhuys and Hanski noted in their 2005 review (*see* also van Nouhuys & Hanski 2004), the Glanville fritillary in the Åland Islands is embedded in complex, multispecies assemblages that include: several plant host species, polyphagous herbivores that are potential competitors, primary parasitoids that attack the butterfly, hyperparasitoids that in turn attack them, a diffuse and shifting ensemble of infectious diseases (e.g., Laine & Hanski 2006), and generalist arthropod and vertebrate predators. The metapopulation dynamics of the Glanville fritillary butterfly leads naturally to metapopulation dynamics in the specialist parasitoids it supports (e.g., Lei & Hanski 1997). Ilkka and his lab used the Glanville fritillary butterfly system to show that such spatial dynamics could facilitate the coexistence of two competing specialist parasitoids, both sustained by their fritillary host (Lei & Hanski 1998, van Nouhuys & Hanski 2002, van Nouhuys & Punju 2010), due to a trade-off between competition and dispersal ability. The host butterfly in turn utilizes two host plant species which differ in quality, with emergent effects on butterfly colonization and hence its colonization–extinction dynamics (Hanski & Singer 2001). One important issue alluded to in the 2005 contribution is the potential role of evolutionary dynamics in governing metacommunity dynamics (*see* also below).

Apparent competition in patchy environments

When I first met Ilkka, some decades past, one theme we discussed (but never followed up on) at the interface of metapopulation dynamics and community ecology was the interplay of direct competition and apparent competition in spatially heterogeneous environments. One of the very first theoretical papers Ilkka wrote (Hanski 1981) had to do with how predation influenced coexistence between species. Back in the 1960s and early 1970s, many ecologists uncritically assumed that predation in some sense generically boosted the number of species that could coexist in a local community. But in the 1970s it was recognized that the relationship of species coexistence to predation was more complex; in some situations, predation had no effect on coexistence, whereas in others, it hampered coexistence. Leigh Van Valen (1974: 18) had earlier argued that "Equivalent predation on all species cannot plausibly increase the number of species of prey," and Abrams (1977) noted that indiscriminate predation could increase the amount of niche differentiation required for resource competitors to coexist. Chase *et al*. (2002) provided an overview of how predation could modulate competitive interactions.

Moreover, if predators can respond numerically or in activity levels to their prey, shared predation could lead to an emergent competitive interaction (apparent competition) between alternative prey (Holt 1977, Holt & Kotler 1987), which could lead to exclusion among prey species that would otherwise not interact. In later years, a really nice experimental study in the Åland Islands (van Nouhuys & Hanski 2000) demonstrated apparent competition: a primary specialist parasitoid (*Cotesia melitaearum*) of the Glanville fritillary butterfly declined when a second primary parasitoid (*C. glomerata*) was added to the system, not because of competition for resources (*C. glomerata* attacks a different butterfly family), but because of a boost in attacks by a shared hyperparasitoid, *Gelis agilis*.

But this tendency towards exclusion could be mitigated if predators ignored prey that were rare (Holt 1977: 215–216), or if prey were spatially segregated and predators either moved at low rates among patches, or adjusted their foraging so as to lead to an approximately "ideal free" distribution of predators across space (Holt 1984) (one way this pattern could emerge is if predators tended to spend more time in patches with more prey). Moreover, theoretical work (e.g., Holt & Kotler 1987) suggested that shared predation could in some circumstances lead to indirect commensalism and even apparent mutualism, because of weak aggregative or reproductive numerical responses, prey refuges, and saturating functional responses. Again, an elegant field experiment in Ilkka's lab in the Åland Islands (van Nouhuys & Kraft 2011) revealed this effect; there is an indirect commensalism between *Melitaea cinxia* and *M. athalia*, in that at a fine spatial scale, the former enjoyed reduced parasitism when the second species was present. These authors also observed that at broad spatial scales, the presence of the second host could boost the occupancy and abundance of the shared parasitoid, and thus lead to apparent competition at large (but not small) scales. There thus can be a scale dependency in the qualitative nature of interactions among species (as noted on purely theoretical grounds in Holt 1987).

What Ilkka pointed out in Hanski (1981) was that the theoretical literature on competition, predation, and species coexistence had largely assumed spatially homogeneous environments, where both predators and their prey were in a certain sense "well-mixed." He then developed a model in which there is a patchy habitat structure, and local density dependence occurs at the patch scale. Within-patch competition was assumed to be linear (on a per capita basis), so in each patch a Lotka-Volterra competition model holds. If densities are homogeneous across space, then the existence of patchiness is irrelevant to competitive coexistence, if local interaction coefficients are spatially invariant. But as Ilkka noted, there is almost always spatial variance in abundance, even if the environment is physically homogeneous. So in the 1981 model he assumed that there is variability in local density within each prey species, across patches, and a well-known empirical relationship between average local abundance and variance in such abundance was assumed to operate within each species. The two prey species were assumed to be both patchily and independently distributed in space (i.e., their spatial covariance in abundances was approximately zero, as often observed in nature), and to experience comparable per capita predation rates within each patch. Ilkka defined "equivalent predation" as resulting from a "process of similarly searching for prey individuals regardless of species, both at the within-patch and between-patch level." This was not the same as random foraging — predators were assumed to forage non-randomly and adaptively among patches, focusing their attention on whichever patches had the greatest total prey abundance. He showed that with these assumptions, equivalent predation could at times actually facilitate coexistence. (This meaning of "equivalent predation" may not match usage of the term in other papers, in that predators in

Hanski's 1981 model would focus attacks on whichever patches had the higher summed abundance, which could be dominated by the prey species with higher overall abundance; however, the assumption is that within patches, predators do not discriminate between prey species).

One thing that strikes me in reading this paper again is how many of its themes resonated through Ilkka's career. There is of course an emphasis on the consequences of spatial patchiness for population processes. Beyond that, however (as in the rodent cycle work summarized above), there is an interest in placing population dynamics in the broader context of community interactions (here, both competition and predation), and paying attention to sensible assumptions about organismal biology (e.g., foraging by adaptive predators). Moreover, Ilkka had an abiding interest in the persistent coexistence of similar, competing species, and in how resource patchiness and spatial processes leading to aggregation could facilitate coexistence (i.e., Kuusela & Hanski 1982, Kouki & Hanski 1995). Indeed, one of his last publications (Ruokolainen & Hanski 2016) developed a novel mechanism whereby reproductive interference among species could reduce their spatial correlation, permitting the coexistence of ecologically identical competing species. Finally, as in so very many of his papers, there is a conceptual elegance, and a willingness to take simplifying (but reasonable) assumptions that lead to biologically interpretable results.

Returning to the 1981 piece, Ilkka assumed that predator numbers were fixed, which allowed him to portray the impact of predation upon the competitive interaction as a shift in isoclines in a two-dimensional phase space. He does note (p. 310) that "Obviously, a model including a dynamic equation for the predator population would be preferable." Ilkka and I talked when we first met in person (I think it was around 1990, at Silwood Park in the UK) about combining our interests in patchiness, predation, and species coexistence, starting with the ideas of his 1981 paper broadened to include numerically responsive predators, and including ideas from a couple of my own papers (Holt 1984, 1987) and his own (Hanski 1983b), but we never got around to doing so.

So in honor of the memory of those conversations, I decided to go back to the model of Hanski (1981), add a predator with a numerical response (in the simplest manner), and now to assume that the prey do not directly compete between species, but instead experience direct intraspecific density dependence, and also apparent competition via the numerical response of their shared natural enemy (as Ilkka and I intended to do back then). The basic approach is what we would have done at that time, and the derivation of the model follows that of Hanski (1981). Using the same assumptions as presented there, we have for local interactions between species n and m in patch i ($i = 1, S$):

$$\begin{aligned} \frac{1}{n_i}\frac{dn_i}{dt} &= r_n\left(\frac{1-n_i}{k_n}\right) - cp_i n_i \\ \frac{1}{m_i}\frac{dm_i}{dt} &= r_m\left(\frac{1-m_i}{k_m}\right) - cp_i m_i \end{aligned}, \qquad (1)$$

where the quantities n_i, m_i, p_i are respectively the densities of two prey species, and their shared predator, in patch i. The parameters r and k are intrinsic growth rates and carrying capacities, indexed for each prey species; the quantity c is the per capita attack rate by the predator, assumed equal for the two prey.

We now follow Ilkka's derivation. Let

$$N = \sum_{i=1}^{s} n_i \text{ and } M = \sum_{i=1}^{s} m_i,$$

and assume that for each prey species, the variance in abundance among patches increases with mean abundance according to

$$\mathrm{var}(n) = a(\bar{n})^2 \text{ and } \mathrm{var}(m) = b(\bar{m})^2,$$

where the overbar denotes average local density. So more abundant species are also more aggregated. Also, we assume that the covariance in abundance between the two prey species is approximately zero. Both these assumptions about spatial variances and covariances seemed to match much empirical data (Hanski 1980, 1981). It would be valuable to explore the current state of these relationships. Peter Abrams (pers. comm.) suggests that in the limit of very low prey density, this empirical relationship might change (between mean and variance of abundance), because all individuals of a species should tend to be found in the best patch, if they have adaptive behavior; he also suggests that there might be positive covariance between species that are similar enough to be consumed by the same predator. However, for our present purposes, we will retain the assumption made in Hanski (1981).

Because we are interested in apparent competition, we set the competition coefficients to zero, and add an equation for the numerical response of the predator. We contrast two kinds of predators, each with a simple local linear functional response to each prey species.

The first predator moves rapidly and indiscriminately among patches, so its density is approximately the same everywhere. After some manipulations, we arrive at:

$$\begin{aligned}
\frac{d\bar{n}}{dt} &= r_n\left[1-\frac{(1+a)\bar{n}}{k_n}\right]\bar{n}-c\bar{p}\bar{n}\\
\frac{d\bar{m}}{dt} &= r_m\left[1-\frac{(1+b)\bar{m}}{k_m}\right]\bar{m}-c\bar{p}\bar{m}\cdot \qquad (2)\\
\frac{d\bar{p}}{dt} &= ce(\bar{n}+\bar{m})\bar{p}-\mu\bar{p}
\end{aligned}$$

The first term in each of the two prey equations corresponds to eq. 11 in Hanski (1981), with interspecific competition turned off, and a simplified predation term. Because the predator is uniformly distributed across patches, the mortality it inflicts on each prey fits a mean-field assumption. The predator has a linear numerical response to the average density of prey across the landscape, and has a constant per capita mortality rate of μ. Finally, each consumed prey produces e predators.

We assume that prey species n has the higher intrinsic growth rate. In general, this gives an advantage to a species in apparent competition (Holt & Lawton 1994), both because a species can thereby better withstand predation pressure, and also because it can thereby sustain high predator numbers (productivity at lower levels flows through to upper levels). We assume that the predator and prey species n are present and at equilibrium, so the average local abundance of the predator is

$$\bar{p}^* = \frac{r_n}{c}\left[1-\frac{(1+a)\mu}{eck_n}\right].$$

Prey species m can invade when rare (so that one can neglect its own direct density dependence), if and only if

$$r_m > c\bar{p}^* = r_n\left[1-\frac{(1+a)\mu}{eck_n}\right]. \qquad (3)$$

The fraction in brackets on the right-hand side describes how much lower the intrinsic growth rate can be for prey species m, than species n, and still permit coexistence of the two prey species. Patchiness and increased aggregation in the resident prey species (increasing a) intensifies intraspecific density dependence. This in effect reduces the productivity that can flow through to the predator, sustaining its abundance. Reducing predator abundance weakens apparent competition. So patchiness and prey aggregation relax constraints on coexistence that arise from apparent competition, even if a predator moves indiscriminately across space.

Ilkka in his 1981 paper made a different and clever assumption about predator behavior. Rather than moving indiscriminately, he argued that one should expect predators to tend to aggregate where they have greater rewards, which with the assumptions of the model (equal attack rates and predator mortality across space), implies they tend to aggregate where total prey abundance is greatest. One of the models in Holt (1984) also assumed such adaptive predator behaviors, but allowed predators to be ideal-free in their habitat use. Ilkka by contrast reasonably assumed that predators move adaptively, but are not necessarily perfectly optimal in their habitat choice. In particular, he assumed that local predator abundances approximately match local prey abundances, so that $p_i \approx q(n_i + m_i)$. This assumption implies a spatial covariance between local predator abundance and local prey abundance. This affects both the growth dynamics of the prey, and of the predator, as follows (the quantity q drops out of the model):

$$\begin{aligned}
\frac{d\bar{n}}{dt} &= r_n\left[1-\frac{(1+a)\bar{n}}{k_n}\right]\bar{n}-c\left(\bar{p}+\frac{a\bar{p}\bar{n}}{\bar{n}+\bar{m}}\right)\bar{n}\\
\frac{d\bar{m}}{dt} &= r_m\left[1-\frac{(1+b)\bar{m}}{k_m}\right]\bar{m}-c\left(\bar{p}+\frac{b\bar{p}\bar{m}}{\bar{n}+\bar{m}}\right)\bar{m}. \qquad (4)\\
\frac{d\bar{p}}{dt} &= ce(\bar{n}+\bar{m})\bar{p}+\frac{ce(a\bar{n}^2+b\bar{m}^2)}{\bar{n}+\bar{m}}\bar{p}-\mu\bar{p}
\end{aligned}$$

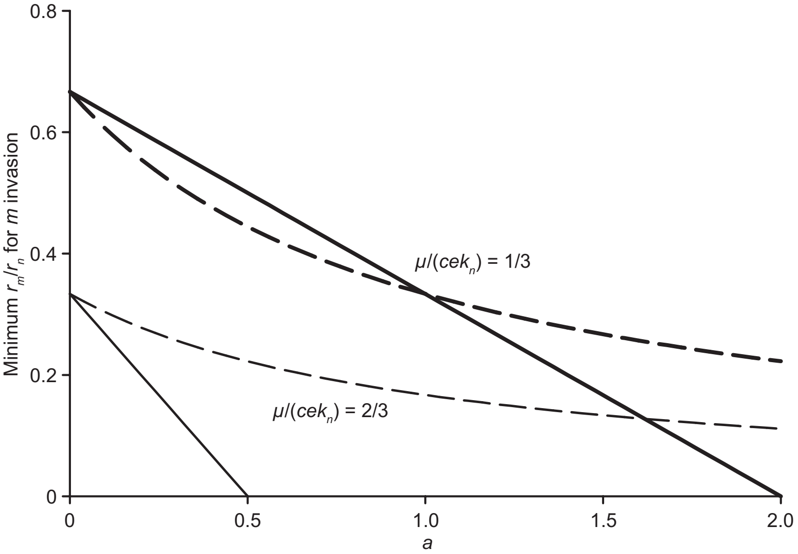

Fig. 1. The condition for invasion of species *m* when it is rare and species *n* is at equilibrium with the predator for the model of Eqs. 2 and 4. Species *m* can invade when r_m/r_n is above each curve. Solid lines are for a randomly attacking predator, while dashed lines are for a predator whose density is proportional to the local total prey density (as in Hanski 1981). For a high value of $\mu/(cek_n)$, invasion is always easier with the random predator, while for small $\mu/(cek_n)$ and low *a*, invasion is easier for the aggregating predator (thick dashed line below the thick solid lines), while for higher *a*, invasion is easier with the random predator.

As before, we assume that prey species *m* is rare and attempting to invade, and prey species *n* and the predator are at equilibrium.

Predator density is now

$$\bar{p}^* = \frac{r_n}{c(1+a)}\left[1 - \frac{\mu}{eck_n}\right]$$

and so the criterion for prey species *m* to invade becomes

$$r_m > c\bar{p}^* = \frac{r_n}{c(1+a)}\left[1 - \frac{\mu}{eck_n}\right]. \qquad (5)$$

Once again, aggregation in the resident prey makes it easier for a prey species with a lower intrinsic growth rate to invade; the right-hand sides of Eqs. 3 and 5 decrease with increasing *a*. However, the reason is different than with a uniformly distributed predator. Because predators differentially attack high-density prey patches, density dependence in the resident prey is weakened, which boosts predator numbers. However, there is a countervailing effect, which is a reduction in the maximal number of predators that can be sustained, when predation is intense (e.g., high *c*), in effect because of an increase in the average attack rate.

The parameter "bandwidth" (*sensu* Armstrong 1976) permitting prey coexistence differs between the predator movement scenarios (*see* Fig. 1). At low values of the prey aggregation parameter *a*, in some cases adaptive foraging by the predator facilitates prey coexistence, compared to a uniform predator distribution. But at higher values of *a*, density dependence in the resident prey strengthens, which for an indiscriminate predator eventually precludes its own persistence. In this case, exclusion due to apparent competition will not occur for such a predator, when it still conceivably could (for prey with quite low *r*'s) for the adaptively foraging predator.

One way to characterize the equilibrium is to examine the shape of the predator isocline, which defines the possible combinations of prey densities at which the system equilibrates. As noted in Holt (1977), if the predator isocline has a negative slope, there is necessarily an apparent competition relationship between the two prey species in their equilibrial abundances. However, some multi-prey–predator models can lead to isoclines that bulge away from the origin, or even have positive slopes, if predators have suboptimal foraging strategies (Holt 1983). Figure

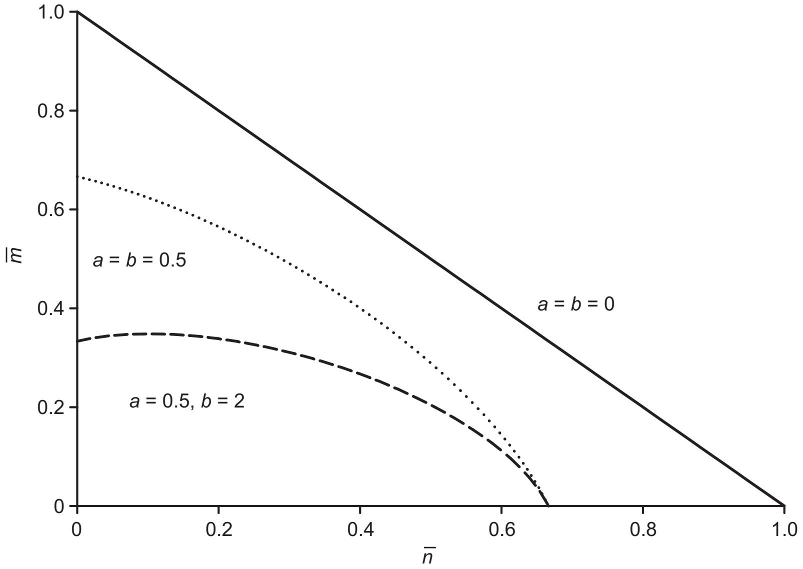

Fig. 2. Predator isocline for the Hanski (1981) model with a dynamic aggregating predator (Eq. 4) with $c = 1$ and $\mu = 1$. (The straight line with $a = b = 0$ also describes the predator isocline for the indiscriminately foraging predator, Eq. 2 in text.) The predator increases for $\bar{m}$ and $\bar{n}$ above the isocline. It is easier for the predator to increase with higher prey aggregation (higher a and b), which pushes the isocline closer to the origin.

2 shows the isocline shapes for the two predator scenarios of models of Eqs. 2 and 4. For the case of a predator moving indiscriminately across the landscape, if both prey can coexist, the equilibrium will lie along the predator isocline, and each prey species will have a lower abundance, than it would enjoy, were it alone with the predator. In other words, apparent competition still exists, even though the prey coexist. A comparable predator which responds to total prey numbers by aggregation has an isocline shifted towards the origin, so overall, prey densities at equilibrium will be reduced. However, the isocline can now bow outwards for some parameter values. This implies the potential not just for a weakening of apparent competition, but the potential for (+,–) interactions (as assessed by say removal experiments) (Holt 1983).

The bottom line is that in a patchy environment, this phenomenological model suggests that prey aggregation tends to weaken apparent competition between prey species, and thus facilitates coexistence, and can even lead to emergent alternative modalities of indirect interactions, depending on how predators respond to prey aggregation. However, other analyses of the interaction between aggregation and prey coexistence in more recent years suggest that this conclusion should be viewed cautiously, as it depends on the details of the explicit rules governing predator movement behavior, the dynamic rules governing the generation of prey aggregation in the first place, the relative values of the two prey to the predators, and other factors. For instance, Abrams (1999) explored a model where predators adaptively moved between two patches, each with a distinct prey species. Adaptive predator switching was shown to potentially lead to strong apparent competition, when the prey exhibited asynchronous dynamics. One assumption made in the above model (building on that in Hanski 1981) is that there is a particular relationship between mean prey abundance and variance among patches in prey abundance, and zero covariance between alternative prey species' abundances. But these attributes of prey abundance themselves are likely to be altered by the pattern of predator movements and attacks. Kilpatrick and Ives (2003) even argue that Taylor's law (a power-law relation between the variance and mean of a species' abundance) may emerge from interspecific interactions. In future studies, it would be valuable to explicitly link dynamical models of interacting predators and prey moving in a patchy environment to emergent statistical properties of the patch ensemble, such as analogs of Taylor's law, and the temporal and spatial correlation structure of across-species abundances. These issues are also ripe for focused empirical study.

Eco-evolutionary dynamics and food chain length

Ilkka had a long-standing interest in the genetic and evolutionary dimensions of ecological processes, an interest which grew and transformed over time. His 1998 paper in *Nature* on inbreeding and extinction risk (Saccheri *et al*. 1998) highlighted how inbreeding by depressing local fitness could exacerbate extinction (*see* also Nieminen *et al*. 2001). This interest developed in many directions in the last decades of his life, for instance with analyses of the evolution of dispersal (Heino & Hanski 2001, Singer & Hanski 2004, Hanski *et al*. 2006, Hanski & Mononen 2011), elucidation of the genetic bases and environmental influences for variation in dispersal (Haag *et al*. 2005, Hanski *et al*. 2006, Zheng *et al*. 2009, Mattila & Hanski 2014, Wong *et al*. 2016), and examination of the interplay of local adaptation and metapopulation processes (Hanski & Heino 2003, Hanski *et al*. 2011).

Again, Ilkka and I often talked about how the interplay of genetics, evolution, and ecology could bear on a wide range of topics, such as patterns in community structure at broad spatial scales. The basic idea was that local evolutionary dynamics should influence colonization and extinction rates (as seems to hold in the Glanville fritillary), and thus patterns of species occupancies in metacommunities. Interactions between species could be a prime driver of local selection, and if such selection corresponded to shifts in population abundance or stability, this could translate into altered colonization and extinction rates across a food web. In turn, how interacting species were co-distributed across space would influence spatial variation in selection, and shifting patterns in abundance could likewise modulate the availability of genetic variation in traits governing fitness, as well as the magnitude of nonselective forces such as gene flow, inbreeding and drift on local adaptation and thus population sizes.

All these effects could have community-level consequences. The Glanville fritillary utilizes different host plants, and selection on host plant use alters its extinction–colonization dynamics. This could have consequences for the colonization-extinction dynamics of dependent, specialized parasitoids, which are already known to be influenced by host diet (van Nouhuys & Hanski 1999). A lovely empirical study (Farkas *et al*. 2013) demonstrated that maladaptation in stick insects due to gene flow in a mosaic landscape permitted greater visitation by birds onto particular local habitats, which then inflicted higher mortality on other resident species of insects in those habitats — an example of apparent competition facilitated by gene flow. So the interplay of evolutionary dynamics and spatial processes could lead to novel community-level consequences in food webs.

A classic problem in community ecology is to understand the factors governing the length of food chains (Hutchinson 1959, McGarvey *et al*. 2016). In several publications, I have argued that for specialist consumers, spatial dynamics could be important in constraining food chain length (e.g., Holt 1997, 2010), and some empirical systems provide suggestive evidence that such effects indeed matter (e.g., Komonen *et al*. 2000, Roslin *et al*. 2014). One idea Ilkka and I played with (but never got around to pulling together) was that evolutionary dynamics (e.g., local adaptation) in predator–prey interactions could influence colonization and extinction rates in ensembles of trophically interacting species, and thus influence food chain length (and other food web metrics). We talked about extending a specific model presented in a chapter in a book Ilkka edited (Holt 1997). A simplified version of eq. 8 in that publication is as follows:

$$dH/dt = cH(1 - H - P) - c_p HP - eH, \tag{6}$$

$$dP/dt = c_p HP - e_p P. \tag{7}$$

Here, H is the fraction of patches that only have prey, and P is the fraction of patches with both the predator and its prey. Prey colonize empty patches at a rate defined by c, and go extinct at rate e. Predators colonize prey patches at rate c_p, and go extinct at rate e_p; such extinctions could occur because the predators over-exploit prey, so that both go extinct, or because prey go extinct for other reasons, and the predators are dragged to their doom with them.

For the prey to persist on its own requires that $1 > e/c$. Given that the prey is present at its equilibrial occupancy of $H^* = 1 - e/c$, the predator can persist if and only if

$$1 > e/c + e_p/c_p. \quad (8)$$

Comparing these inequalities shows that there could well be metapopulations that sustain the prey species, but not the specialist predator which depends upon it. There are some excellent examples matching this prediction in the Glanville fritillary (van Nouhuys & Hanski 2005).

So in honor of past conversations with Ilkka about extending such models to incorporate eco-evolutionary dynamics, in the next several paragraphs I will present a simple model in which local adaptation by a prey/host species to a predator/pathogen can influence occupancy of the latter (in the simplest possible "food chain," namely a bitrophic interaction). As Ilkka often emphasized, the intellectual roots of metapopulation ecology are in island biogeography (Hanski 2004). In classic metapopulation and metacommunity models, rather than track individual populations sizes, genotype frequencies, and the like, one imagines that each site in a metacommunity can be characterized by a "state" defined by the presence/absence of different combinations of species (as in Eqs. 6–7 above). Transitions among these states of course include colonization, extinction — and now, we will assume, local, within-patch, adaptation by the victim species to its natural enemy, as well.

In homogeneous systems, it is becoming increasingly appreciated that there can be a wide range of potential consequences of local evolution on population dynamics of interacting predators and prey (Hairston *et al*. 2005). For instance, evolution can lead to longer periods in predator–prey cycles, thus increasing the length of time species are at low densities. Abrams and Matsuda (1997) explored a predator–prey model in which prey adapted to predation, at a cost to their intrinsic growth rate. In the absence of such evolution (in the example shown in Hairston *et al*. 2005), the populations settle to a stable equilibrium. With evolution in the prey, pronounced population cycles arise, so that periodically predators collapse to low density because the prey have evolved to escape predation; when predation is low, prey defense wanes, allowing predators to eventually rebound. The local dynamics explored by Abrams and Matsuda (1997) (among others, e.g., Jones *et al*. 2009) can be embedded in a spatial context, and have implications for both extinction and colonization dynamics. Populations that cycle spend periods at low densities, with elevated extinction risks. And changes in local abundance due to evolutionary dynamics can alter the number of propagules available for colonizing empty patches from occupied patches.

I will make some specific assumptions. As in Eqs. 6–7, a patch that is empty can be colonized by a prey species, but not the predator. A patch occupied by a prey species may experience extinction, persist unchanged, or be colonized by a predator. Once the predator is present, however, the prey can then adapt to its presence. If the prey adapts sufficiently so as to avoid predation, the predator on that patch may end up at such low abundance that it rapidly goes extinct (e.g., at the low trough in abundances in the predator–prey cycles of the Abrams-Matsuda 1997 model). Or, the prey may adapt, and the predator still persists for a while, albeit at such low densities that it ends up going extinct. One question that immediately arises in either case is: what is the relationship between adaptation by prey to avoid predation, and the realized length of food chains across all patches (in comparison say to the expectations from the non-evolutionary model above)?

We assume that there is an exponentially distributed "waiting time" for a prey population exposed to predation to adapt to the predator. Prey populations can fall into several states: the prey can be present alone on a patch, but not adapted to the predator; or, the predator can be present, with the prey in a non-adapted state; or, the prey can have adapted to the predator. Adapted patches with predators can lose those predators, and the prey population there can then revert to a non-adapted state (*viz*., because anti-predator adaptations are costly).

A metapopulation model incorporating adaptation by prey to shake off the predator is as follows:

$$\begin{aligned} dH/dt &= cH(1 - H - P - H') - c_pHP + rH' - eH \\ dP/dt &= c_pHP + e_pP - aP. \\ dH'/dt &= aP - rH' - e'H' \end{aligned} \quad (9)$$

The quantity H' is the fraction of patches with prey that have adapted to the predator, which happens at rate a. We assume that the number of colonizing individuals moving among patches is always small, relative to local average abundances, post-colonization (this way we can to a first approximation neglect complications due to gene flow swamping local selection), and also that if predators happen to persist on patches with adapted prey, these predators are scarce and so negligible as sources of colonists into available patches with non-adapted prey. (Such patches would have an effective food chain length of unity.) Predator colonization thus only occurs from patches where prey are still not adapted to predation. Likewise, we assume that patches in which prey have adapted to predators are not able to directly send prey colonists to empty patches. This could occur if for instance there were a strong trade-off between dispersal ability, and ability to escape predators within patches. Eventually, we assume that predators disappear from these adapted-prey patches. After the predators are gone, the selective costs of anti-predator adaptations are not matched by any benefits, and over time (again, exponentially distributed), these patches lose anti-predator adaptations, re-enter the pool of vulnerable prey patches (at rate r) and again can contribute colonists to the metapopulation.

With these assumptions, the condition for the predator to invade when rare, and the prey is at equilibrium, becomes

$$\frac{e}{c}+\frac{e_p+a}{c_p}<1. \tag{10}$$

Reversing this inequality characterizes metapopulations where the predator cannot increase when rare. Permitting prey to adapt to the predator removes (by our assumptions) those patches from the dynamically relevant part of the predator metapopulation, and hence makes it harder for the predator to persist. Comparing the expressions for predator invasion shows that prey adaptation makes it harder for the predator metapopulation to persist.

Numerical examples are presented in Figs. 3 and 4. We start with a prey metapopulation occupying most of the landscape, and assume that the prey is for a while not able to adapt to predation. The predator invades, and after a period of damped oscillations, settles into a system where most occupied patches have both predator and prey. At t = 100, we allow adaptation to begin, but adapted patches neither recover, nor colonize other patches. There is a transient phase of increase in adapted patches, which leads to a rapid decline in occupancy by the predator. In some cases (Fig. 3), the predator persists, as does a mix of patches, some with maladapted prey, and some with adapted prey. In this case, we then allow adapted hosts to lose their adaptation (starting at t = 200), which leads to an equilibrium with fewer adapted patches and the same number of adapted patches. The number of predator patches increases to a level slightly higher in overall occupancy of the landscape than before adaptation started, basically because allowing the prey to adapt to the predator, and also to lose that adaptation once the predators are gone, permits a replenishment of susceptible prey patches the predator can colonize. So prey adaptation can boost food chain length a bit, in this example.

In other cases (Fig. 4), rapid adaptation by the prey leads to a sharp decline in predator occupancy, and ultimately predator extinction. Predator exclusion occurs not because prey are persistently adapted to avoid predation, but because they can quickly, locally adapt to predation, reducing the predator's ability to colonize other patches. Rapid prey evolution can thus lead to a kind of dynamic, transient exclusion of a specialist predator.

The basic conclusion of these simple models is that prey adaptation to withstand predation should be able to influence food chain length on islands, but that whether or not it is expected to shorten or lengthen food chain length depends on how such adaptation translates into impacts on extinction and colonization rates. Moreover, the potential for prey adaptation may permit predators to be excluded from a metapopulation, even if a snapshot assessment of prey traits in the predator-free landscape (where the prey is expected not to be adapted to avoid this specific predator) might suggest that the predator could successfully establish.

This metapopulation model is akin to models in epidemiology, where hosts are classified into discrete states, such as susceptible, infected, and resistant (SIR models). In a sense, the evolu-

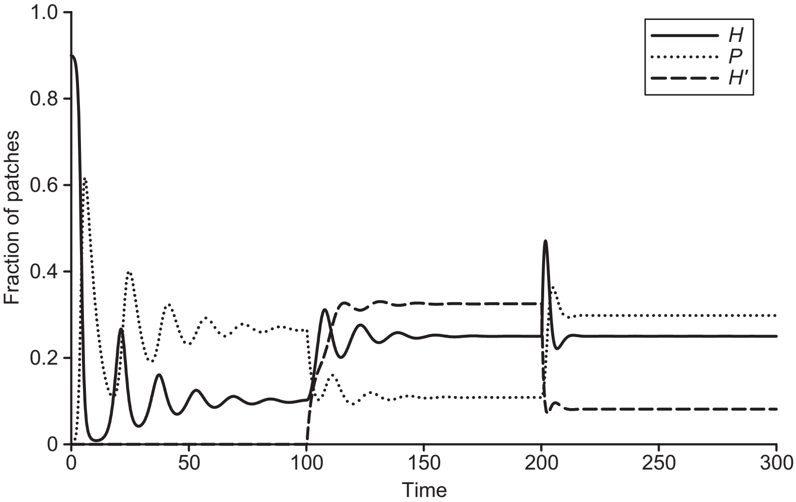

Fig. 3. Fraction of patches occupied by the original host (H), this host and the predator (P) or the adapted host (H') for the metapopulation model of Eq. 9. Initially, the host is at its equilibrium if alone ($H = 0.9$), the predator fraction is $P = 0.001$ and there are no adapted hosts ($H' = 0$). For $t < 100$, the parameters are $c = 1$, $c_p = 2$, $e = 0.1$, $e_p = 0.2$, $e' = 0.1$, $a = 0$ (so there is no host adaptation) and $r = 0$. At $t = 100$, the hosts become able to become adapted, so $a = 0.3$ thereafter. At $t = 200$, adapted hosts become able to lose adaptation, so r goes to 1. Adaptation causes the predator fraction to decline, which allows the non-adapted host patches to increase along with the adapted host patches. Loss of adaptation causes the adapted patches to drop and the predator patches to increase (with no effect on non-adapted host patches).

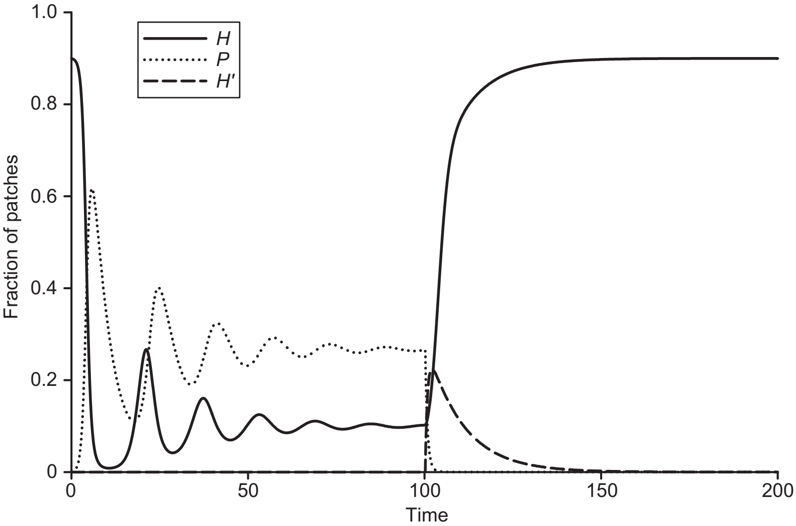

Fig. 4. Fraction of patches occupied by the original host (H), this host and the predator (P) or the adapted host (H') for the metapopulation model. Initially, the host is at its equilibrium if alone ($H = 0.9$), the predator fraction is $P = 0.001$ and there are no adapted hosts ($H' = 0$). For $t < 100$, the parameters are $c = 1$, $c_p = 2$, $e = 0.1$, $e_p = 0.2$, $e' = 0.1$, $a = 0$ (so there is no host adaptation) and $r = 0$. At $t = 100$, the hosts become able to become adapted, so $a = 1.6$ thereafter. In this case, the adaptation rate is high enough to cause loss of the predator (and adapted patches).

tion of anti-predator adaptations embodied in the model above is akin to the development of resistance in an infected host. If such resistance rapidly develops, the R_0 of the infection (*viz*., the number of secondary infections spawned by a primary infection) is pushed below one, which prevents the spread of the infection. In like manner, the rapid evolution of resistance by prey to predation can lower the ability of the predator to increase when rare in a metapopulation, thus leading to the exclusion of predators from a patchy landscape.

There are many ways in which these occupancy models could be elaborated to include other evolutionary and ecological scenarios. Predator–prey interactions are prone to sustained instability, and even asymptotically stable systems can show pronounced oscillations following environmental perturbations, so examining how these issues play out in the context of non-equilibrial dynamics could be of particular importance (P. Abrams pers. comm.). As noted in Holt (1997), at times predators can moderate instability in their prey, and even increase prey abundance (e.g., by preventing overexploitation by the prey of its own resource, a phenomenon related to the "hydra effect" identified by Abrams 2009). Adding evolution can alter these ecological effects, or lead to more complex dynamical behaviors (e.g., Cortez & Ellner 2010, Yamamichi *et al*. 2011). For instance, one might envisage that prey populations that have adapted to the predator could themselves send out colonists into empty patches. (As with our above results, we can assume to a first approximation that immigration into occupied patches is negligible, so can ignore the complications of the interaction of gene flow and selection.) In this case, we could replace the last sub-equation in Eq. 9 with say

$$dH'/dt = aP - rH' - e'H' + c'H'(1 - H - P - H').$$

In a sense, adapted and non-adapted prey populations "compete" for empty patches. It can be shown that if, with no predator and $r = 0$, H eliminates H', then this will also obtain if $r > 0$. Such elimination requires $c/e > c'/e'$; in other words, if there is demographic cost of adaptation to the predator at the metapopulation scale, one expects the predator-free landscape to have prey vulnerable to predation.

The specific conclusions drawn from the model assume in particular that prey so effectively adapt to predators that if they continue to co-occur, the predators cannot send colonists to predator-free patches. An alternative scenario would be that prey weakly adapt to predators by say a modest reduction in attack rates. If predators thereby are less able to overexploit the prey, extinction rates could be lowered by prey evolution, and predator numbers even enhanced. In this case, prey evolution could sustain longer food chains across the metapopulation.

All such model extensions rely upon the simplifying assumption that one can characterize patches into discrete states (e.g., non-adapted prey, vs. adapted prey). This may be a gross and at times misleading oversimplification of systems with complex eco-evolutionary dynamics, for which an explicit accounting of within-patch processes might be needed. For instance, if gene flow among patches can perturb local populations away from their local selective equilibria, much more complex models would be required that pay specific attention to the microevolutionary mechanics of selection, gene flow, and drift in determining local adaptation of prey to predators (and *vice versa*), with emergent impacts on colonization and extinction processes in a metacommunity.

Discussion and conclusions

The basic conclusion I draw from my overview of Ilkka Hanski's contributions to trophic ecology is that they are intellectually expansive and of enduring value. The issue of understanding the contribution of predation as drivers of dramatic oscillations in the abundance of small mammals has not been resolved by his work (Krebs 2013), but to my eyes there is a much stronger case than was available thirty years ago that the interplay of generalist and specialist predators has a special role in observed patterns.

In terms of the specific themes that I wish I had followed in collaboration with Ilkka, there are of course many directions in which both could be pushed. My extension of Hanski (1981) presented above made a number of simplifying assumptions, matching those that he made in that paper. Space is implicit. Stochasticity must underlie spatial variation in prey abundance, but such stochastic sources of variation are likewise implicit. The predator functional and numerical responses within patches are linear. All of these should be relaxed in future analyses of this problem. A contemporary approach to this issue might for instance use individual-based analytic or simulation models, which allow one to include realistic assumptions about predator movement and foraging across explicit landscapes. These models could include heterogeneity in the model parameters themselves, and also incorporate impacts of demographic stochasticity and the details of life histories (e.g., Detto & Muller-Landau 2016, who conjecture that time lags in natural enemy effects could influence the buildup and decay of spatial correlation structures in shared predation systems). Another analytic approach might be to use moment-closure techniques (e.g., Bolker *et al*. 2003) to look explicitly at the dynamics of spatial variances and covariances for each species and set of interacting species. In Holt (1987) I surmised that the sign of indirect interactions between alternative prey species could shift with the spatial scale of investigation. It would be useful to examine this conjecture more forcefully in models with realistic assumptions about predator–prey interactions and spatial dynamics playing out across complex landscapes. One could also add additional species (e.g., a mix of specialist and generalist predators), and examine how this alters expectations about coexistence. The food web dimension of coexistence theory is receiving increasing attention (e.g., Chesson & Kuang 2008), and placing this issue in a spatial context would likely open up new avenues for both coexistence and exclusion in metacommunities.

Metapopulation approaches to understanding food chain length and other attributes of food webs are receiving increasing attention. Gravel *et al*. (2011) provide a valuable way forward in trophic island biogeography by permitting colonization and extinction rates to be defined by whether or not generalist consumers have at least one requisite prey species present on an island. Carrying out comparable analyses in metacommunities, rather than islands, is inherently a more complex problem, in part because of the multiple potential sources of colonization for any particular species. The way in which evolution was represented in the above models is really a cartoon; ideally, one would track explicit gene frequencies of particular loci, or assume quantitative genetics, in each of a number of patches. Islands or patches might be represented as a continuum of evolutionary states, rather than as simply "adapted" or "not adapted," and moreover, all interacting species (not just the prey in the pairwise predator–prey interactions I assumed above) should be allowed to co-evolve in tandem. And dispersal does not merely colonize empty patches, it also couples over evolutionary time scales occupied patches, infusing genetic variation and at the same time pulling local populations away from local optima. It is a very large challenge, splicing together all the separate pieces that are at play in metacommunities — the direct and indirect interactions among a multiplicity of species, the playing out of interactions via dispersal over large landscapes, the reciprocal impacts of these ecological processes on evolutionary dynamics, and the resultant shift in ecological processes because of evolved trait differences — but as we address this challenge over the years to come, I have no doubt that the wonderful foundational work of Professor Ilkka Hanski will continue to resonate.

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