EVOLUTION

Coevolution with hosts underpins speciation in brood-parasitic cuckoos

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Coevolution between interacting species is thought to increase biodiversity, but evidence linking microevolutionary processes to macroevolutionary patterns is scarce. We leveraged two decades of behavioral research coupled with historical DNA analysis to reveal that coevolution with hosts underpins speciation in brood-parasitic bronze-cuckoos. At a macroevolutionary scale, we show that highly virulent brood-parasitic taxa have higher speciation rates and are more likely to speciate in sympatry than less-virulent and nonparasitic relatives. We reveal the microevolutionary process underlying speciation: Hosts reject cuckoo nestlings, which selects for mimetic cuckoo nestling morphology. Where cuckoos exploit multiple hosts, selection for mimicry drives genetic and phenotypic divergence corresponding to host preference, even in sympatry. Our work elucidates perhaps the most common, but poorly characterized, evolutionary process driving biological diversification.

Most species are involved in coevolutionary interactions (*1*), in which closely interacting species impose selection pressures on one another that result in reciprocal evolutionary change. Coevolution can accelerate divergence, particularly in the face of gene flow, and is believed to be such an important mechanism of diversification that it is likely to explain why there are millions, rather than thousands, of distinctly specialized species (*2*). However, despite numerous calls for research, the paucity of evidence linking macroevolutionary patterns to microevolutionary processes driving speciation remains an outstanding empirical gap in our understanding of coevolutionary diversification (*3–6*).

A particularly tractable system for investigating coevolutionary diversification is the brood-parasitic reproductive strategy used by cuckoos that lay their eggs in the nests of other bird species and thereafter abandon their young to the care of the host (*7*). Cuckoos vary in the costs they impose on hosts: In some species, cuckoo chicks evict the host young from the nest (evicting cuckoos), whereas in others, cuckoo chicks are reared alongside the host young (nonevicting cuckoos). This dichotomy in virulence predicts the intensity of selection for host defenses; hosts exploited by chick-killing parasites generally evolve defenses based on recognition and rejection of brood parasite young, whereas those exploited by more benign brood parasites evolve life-history strategies that tolerate the costs of parasitism (*8, 9*). Parasitism that results in the death of host young typically leads to a coevolutionary arms race; parasitism selects for host defenses, such as rejection of cuckoo young, which in turn select for counteradaptations in cuckoos, such as mimicry of host young, that deceive the host into accepting the parasite young (*8, 9*) (Fig. 1A).

When a brood parasite species exploits multiple different hosts, selection for mimicry of the eggs or nestlings of several different host species may drive genetic diversification of the parasite into distinct host-specific lineages, each of which mimics the eggs or nestlings of their respective host (*10*) (Fig. 1B). However, the likelihood that such divergence ultimately results in the generation of new species depends on how mimetic traits are inherited, which differs between cuckoos that mimic host eggs and those that mimic host nestlings (*7*). Successful egg mimicry is achieved through maternal inheritance of egg color in cuckoos (*10, 11*); a female exploits the host that reared her and lays the same egg type as her mother, and the trait is obviously not expressed in sons. By contrast, mimetic traits at the nestling stage cannot be sex linked, as both male and female nestlings must be mimetic to survive. Instead, mimicked nestling traits, such as down feather color and distribution (*12*), skin and flange color (*12, 13*), and call structure (*14*), are complex traits (*15*) that are likely to be inherited from both parents (*7, 16, 17*). Therefore, when a cuckoo species is under divergent selection to mimic the nestlings of several different host species, we would predict assortative mating between males and females that specialize on the same host to reinforce local adaptation within host-specific lineages selected by host defenses. This could generate new, host-specific species (Fig. 1B) (*7*). Moreover, such host-shifts by parasites are predicted to lead to a greater tendency for parasites to speciate in sympatry than nonparasitic organisms, although this is not an inevitable outcome (*18*).

Macroevolutionary evidence that coevolution underpins speciation

Focusing on the subfamily Cuculinae, we began by exploring whether rates of speciation are greater in highly virulent, evicting cuckoos than in nonevicting and nonparasitic cuckoos. We used recently developed methods to quantify speciation rates (cladogenetic diversification rate shift model, ClaDS) (*19*) as well as other tree-based statistics that offer tip-rate estimates (*20*). Our results show that parasitic species that are highly virulent tend to have higher speciation rates on average when compared with species that are parasitic but nonevicting and when compared with nonparasitic species (Fig. 2, A and B, and fig. S1A). This is consistent with previous research, which shows that the most virulent cuckoo species have more recognized subspecies (*21*), and with a simulation model showing that in sympatric host races, host race fidelity should increase over time and gene flow between host races should cease (*22*). We note, however, that given that there is a single origin of high virulence in cuckoos, there is no statistical power to test explicitly whether a parasitic lifestyle is responsible for the increased rates we report.

Further, if coevolutionary interactions between highly virulent cuckoos and hosts promote sympatric speciation of cuckoos, we would expect to see a higher frequency of sympatric speciation among highly virulent cuckoos that are under selection to mimic host young than among other parasitic and nonparasitic cuckoo species. To test this, we used a process-based simulation model to compare the geographic modes of speciation in highly virulent *Chrysococcyx* or *Chalcites* cuckoos [hereafter referred to as *Chrysococcyx/Chalcites*; the only clade in which mimicry of host nestlings has evolved in response to rejection of cuckoo nestlings by hosts (*12–14, 23, 24*)] with other parasitic and nonparasitic cuckoos in the family Cuculidae (*20*). We found the greatest support for the predominant role of sympatric speciation or a mixed model of speciation, which includes a degree of sympatric speciation, in three nested clades of parasitic cuckoos. The support for sympatric speciation increased when considering the most-nested *Chrysococcyx/Chalcites* clade independently (Fig. 2C). The support for sympatric speciation in virulent cuckoos, particularly those of the *Chrysococcyx/Chalcites* clade, is stronger than has been seen in any other bird clades investigated in previous comparative studies (*25, 26*), including for finches in the family Viduidae (*25*), which are one of the most likely candidates for sympatric speciation among birds (*27*). This suggests that support for sympatric speciation is specifically compelling for the *Chrysococcyx/Chalcites* clade of cuckoos. The support for sympatric speciation also stands in contrast to the nonparasitic clades *Coccyzus* and *Coua*, in which we found the greatest
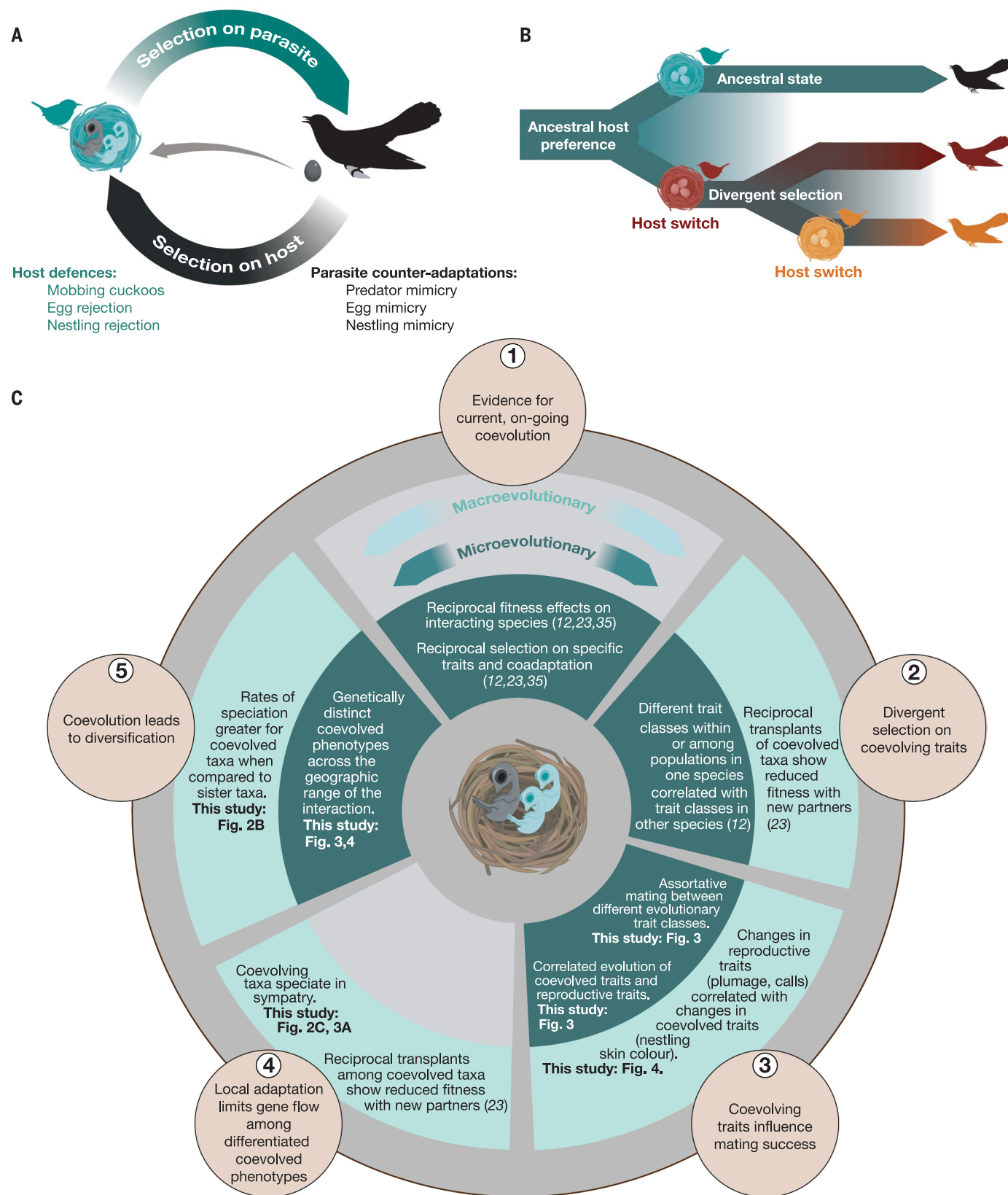
Fig. 1. Processes of coevolutionary diversification in cuckoo-host interactions and evidence from *Chalcites* cuckoos. (**A**) Coevolutionary arms races comprising defenses in hosts (*23, 59, 60*) and counteradaptations in brood parasites (*12, 59, 61*) are proposed to drive (**B**) coevolutionary diversification in brood parasites. (**C**) Evidence of coevolutionary diversification at microevolutionary and macroevolutionary scales [adapted from (*4*)] and the supporting evidence from current work on *Chalcites* spp.
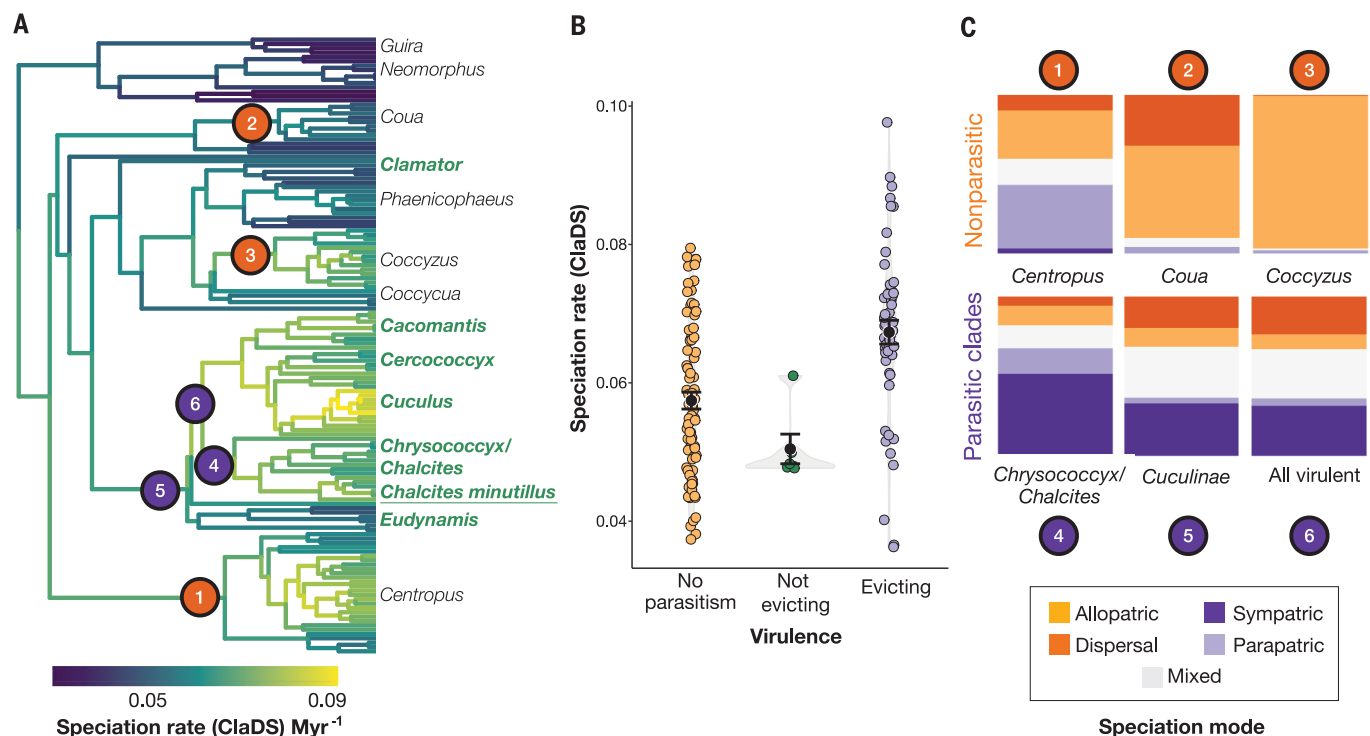
Fig. 2. Macroevolutionary patterns of speciation rates and mode in the Cuculidae. (**A**) Rates of speciation obtained from tip-rate analysis in ClaDS when using the MCC tree (*19*), with parasitic genera shown in bold. Parasitic species tend to show higher rates. Numbers on nodes represent clades used for speciation mode analyses in (C). The phylogeny presented is the maximum clade credibility tree (MCC) from 10,000 phylogenies downloaded from birdtree.org (*62*). (**B**) Comparison of speciation rates for different categories of parasitic lifestyle using the MCC tree. (**C**) Posterior probability of five different models of speciation from approximate Bayesian computation–based inference and linear discriminant analysis. Monophyletic clades used for analyses are indicated with a number in the phylogenetic tree (A).

support for speciation by isolation (allopatric or dispersal modes), and *Centropus*, which shows the greatest support for a predominantly parapatric mode of speciation (Fig. 2C).

Microevolutionary evidence: Focusing in on bronze-cuckoos

To understand the microevolutionary processes driving these macroevolutionary patterns, we investigated coevolutionary diversification in bronze-cuckoos, *Chalcites* spp. (sometimes placed within the *Chrysococcyx* genus), using behavioral, phenotypic, and genetic data. These cuckoos impose heavy costs on their hosts and have evaded host defenses at the egg stage (*28–30*). However, hosts reject cuckoo nestlings, an action which has selected for mimicry of host young by cuckoo nestlings (*12–14, 23, 24*). We focused on two closely related species, the shining-bronze cuckoo *C. lucidus* and the little bronze-cuckoo *C. minutillus*, both of which are host specialists that primarily exploit *Gerygone* spp. of the family Acanthizidae across their range (the Australian subspecies of *C. lucidus* exploits other *acanthizid* hosts) (*31*). *C. lucidus* comprises four subspecies that breed in Australia, New Caledonia, New Zealand, the Solomon Islands, and Vanuatu (*32*). *C. minutillus* comprises 13 subspecies, more than any other brood-parasitic cuckoo (*31*). In Australia, three morphs

are recognized based on subtle morphological differences: a "*minutillus*" form that breeds across northern Australia; a "*russatus*" form, with a distribution that overlaps that of "*minutillus*" in northeastern Queensland; and a "*barnardi*" form that breeds in southeastern Queensland and northern New South Wales (*33, 34*). The taxonomy of these morphs is contentious (*20, 33, 34*), and the factors that promote and maintain divergence, particularly in areas of sympatry, are unknown (*34*).

Evidence of local adaptation to hosts, selected by host rejection of cuckoo chicks

We investigated empirically whether coevolution with hosts underpins speciation in bronze-cuckoos. Rejection of cuckoo nestlings by hosts (*23, 24*) has selected for mimicry of host nestlings by cuckoos (*12*); the nestlings of bronze-cuckoo species mimic the skin, down, and flange color (*12, 13*) and begging calls (*14, 35*) of their respective hosts. We have previously demonstrated that mimicry is driven by coevolution with hosts because host rejection can be triggered by experimental alteration of mimicked traits in both parasite and host young (*36*). We found that average trait values (skin and flange color and morphology of down feathers) of nestling cuckoos are correlated with average trait values of host nest-

lings (*12*). With transplant experiments, we also showed that shining bronze-cuckoos suffer a fitness cost when reared by a secondary host rather than the primary host with which they have coevolved; 100% of nestlings were rejected by the secondary host, which they do not mimic (*23*).

We show an even finer scale of coevolution; selection for mimicry of host nestlings does not only lead to divergent cuckoo nestling morphology among species, but also between sympatric morphs within the same species. In northeast Queensland, the *russatus* and *minutillus* forms occur in sympatry, but it was previously unknown which hosts they exploit or whether their nestlings are morphologically distinct (*37*). We reveal divergent morphology between nestling little bronze-cuckoos reared by the two different hosts. The previously undescribed nestlings of both fairy gerygone (*Gerygone palpebrosa*) hosts and little bronze-cuckoos that were reared by fairy gerygones each have pale skin and a yellow gape flange (Fig. 3B). By contrast, sympatric little bronze-cuckoos reared by large-billed gerygones (*Gerygone magnirostris*) have dark skin and a white flange resembling those of large-billed gerygone nestlings (Fig. 3B) [and to a lesser extent, those of their secondary host, mangrove gerygones (*Gerygone levigaster*)]. The color differences
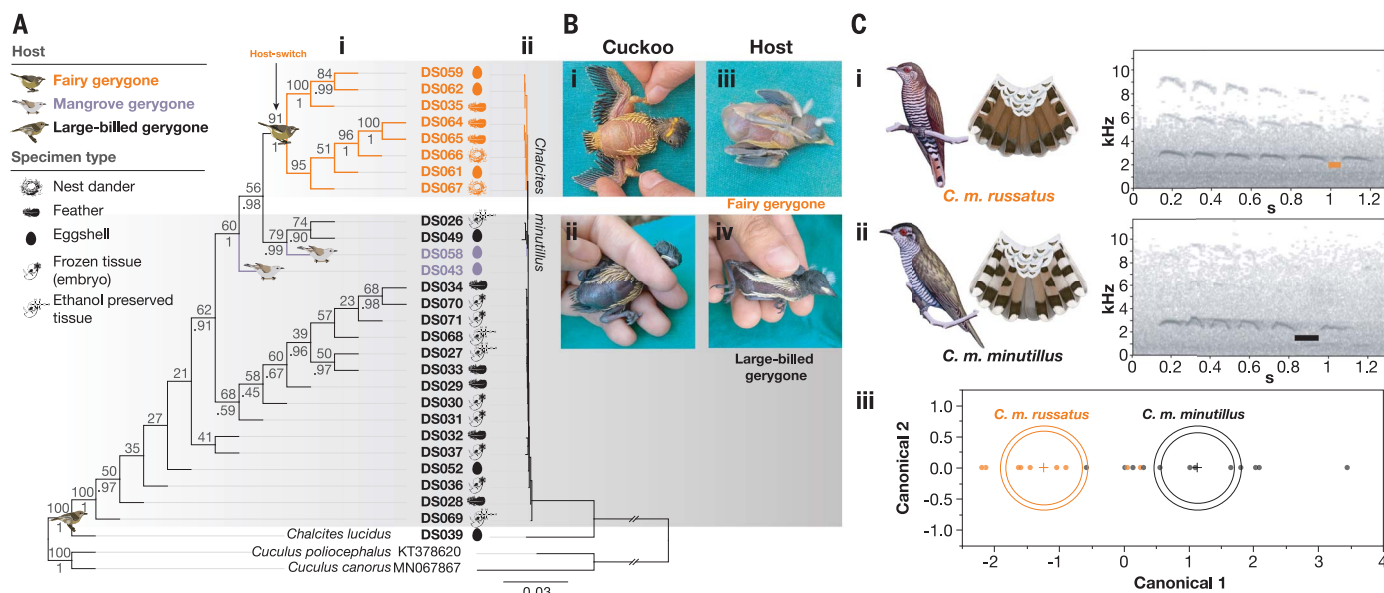
Fig. 3. Little bronze-cuckoos that exploit fairy gerygone hosts are phenotypically and genotypically divergent, showing incipient speciation driven by host specificity. (**A**) (i) Maximum-likelihood whole-mitochondrial phylogenetic tree of 27 little bronze-cuckoo specimens colored according to host preference [mt sequence alignment available at (58)]. Bootstrap support (%) values are indicated above, and Bayesian posterior probabilities are indicated below the node of the cladogram (missing values indicate the topology was not supported). (ii) The phylogram (branch length = nucleotide substitutions per site) is depicted to the right. (**B**) Phenotypic differences between the nestlings of the (i) *russatus* and (ii) *minutillus* morphs. *Russatus* nestlings (N = 5) have pale skin resembling (iii) fairy gerygone nestlings (N = 5 broods), whereas *minutillus* nestlings (N = 180) have dark skin resembling (iv) large-billed gerygone nestlings (N = 123 broods). (**C**) Phenotypic differences between adults of the (i) *russatus* and (ii) *minutillus* morphs. The *russatus* morph shows more rufous plumage than the *minutillus* morph (33) [illustrations: tails, Julian Teh, Commonwealth Scientific and Industrial Research Organisation; adults, J. Davies (33)]. The spectrograms show adult male advertising calls, and the bars indicate the longer pause before the final note in *minutillus* than *russatus*. (iii) Canonical plot showing multivariate mean (indicated by +) of call variables for *minutillus* and *russatus*. The circle corresponds to the 95% confidence limit for the mean. Groups that are significantly different have nonintersecting circles (discriminant function analysis; Wilk's l = 0.39, exact $F_{4,18}$ = 6.91, P = 0.002).

between light and dark morph bronze-cuckoo nestlings have previously been shown by reflectance spectrophotometry and visual modeling to be detectable through a bird's eye (12, 38). Consistent with our finding that *minutillus* nestlings mimic large-billed gerygone nestlings, whereas *russatus* nestlings mimic fairy gerygone nestlings, the distributions of the two cuckoo morphs mirror those of the hosts they mimic; the wider range of the *minutillus* morph corresponds closely with the range of large-billed gerygone hosts, whereas the narrower range of the *russatus* morph matches that of fairy gerygones (37) (Fig. 4).

Genetic divergence between populations corresponds to host use

To test whether these two morphs might represent the early stages of sympatric speciation, we took a molecular genetic approach (20). Evidence to address this question has been lacking because previous genetic analysis of little bronze-cuckoos has been done on adult birds (37) and is thus blind to the host preference of the individual. We targeted the period of the life cycle when host use can unequivocally be ascribed by sampling little bronze-cuckoo eggs and nestlings in host nests in the field (20). Such analyses have been hindered pre-

viously by the difficulties of locating sufficient numbers of parasitized host nests. We added to our field samples by using parasitized clutches of eggs held at the Australian National Wildlife Collection, CSIRO Australia (20), capitalizing on new techniques for DNA extraction from historical eggshells (39, 40). By harnessing 61 years of collecting effort, we report that genetic divergence in little bronze-cuckoos corresponds to host preference (total in situ samples N = 27). Using a hybridization capture approach (hyRAD) (20), we surveyed 8167 restriction site–associated DNA (RAD) loci for 24,889 single-nucleotide polymorphisms (SNPs) (20). Sufficient orthologous SNPs were unable to be recovered across individuals with known host preference owing to the low nuclear DNA content in historic eggshells, so nuclear analyses were restricted to adult specimens for which host preference was unknown (20). However, both maximum likelihood and Bayesian phylogenetic inference of whole mitochondrial genomes reconstructed from off-target reads show that cuckoos parasitizing fairy gerygones form a monophyletic clade with high support (91% bootstrap support, posterior probability 1) (Fig. 3A). Individuals in this clade are more closely related to one another, regardless of geographic distance, than they are to sympatric

little bronze-cuckoos laid in large-billed gerygone nests (Fig. 3A and fig. S6). This result is evidence of host specialization and, given that the multiple complex mimetic traits that are expressed in both male and female nestlings are unlikely to be solely maternally inherited (7, 15–17), it is consistent with assortative mating of little bronze-cuckoos reared by different host species.

Divergent adult plumage and vocalizations and genetic evidence for assortative mating

Furthermore, we included samples from 25 vouchered adult little bronze-cuckoo specimens in the mitochondrial analysis with the goal of linking adult plumage morphs to host specialization behavior (20). All vouchered adult *russatus* morphs had mitochondrial genomes most similar to those of cuckoo nestlings raised in fairy gerygone nests (fig. S11). This is the first unequivocal evidence linking adult plumage to host preference and nestling morphology, again consistent with assortative mating of little bronze-cuckoos reared by different host species. Similarly, most of the *minutillus* morphs clustered alongside cuckoo nestlings raised in large-billed or mangrove gerygone nests (fig. S11). The shallow nature of the mitochondrial phylogenetic tree and the weak nuclear differentiation of vouchered adult plumage
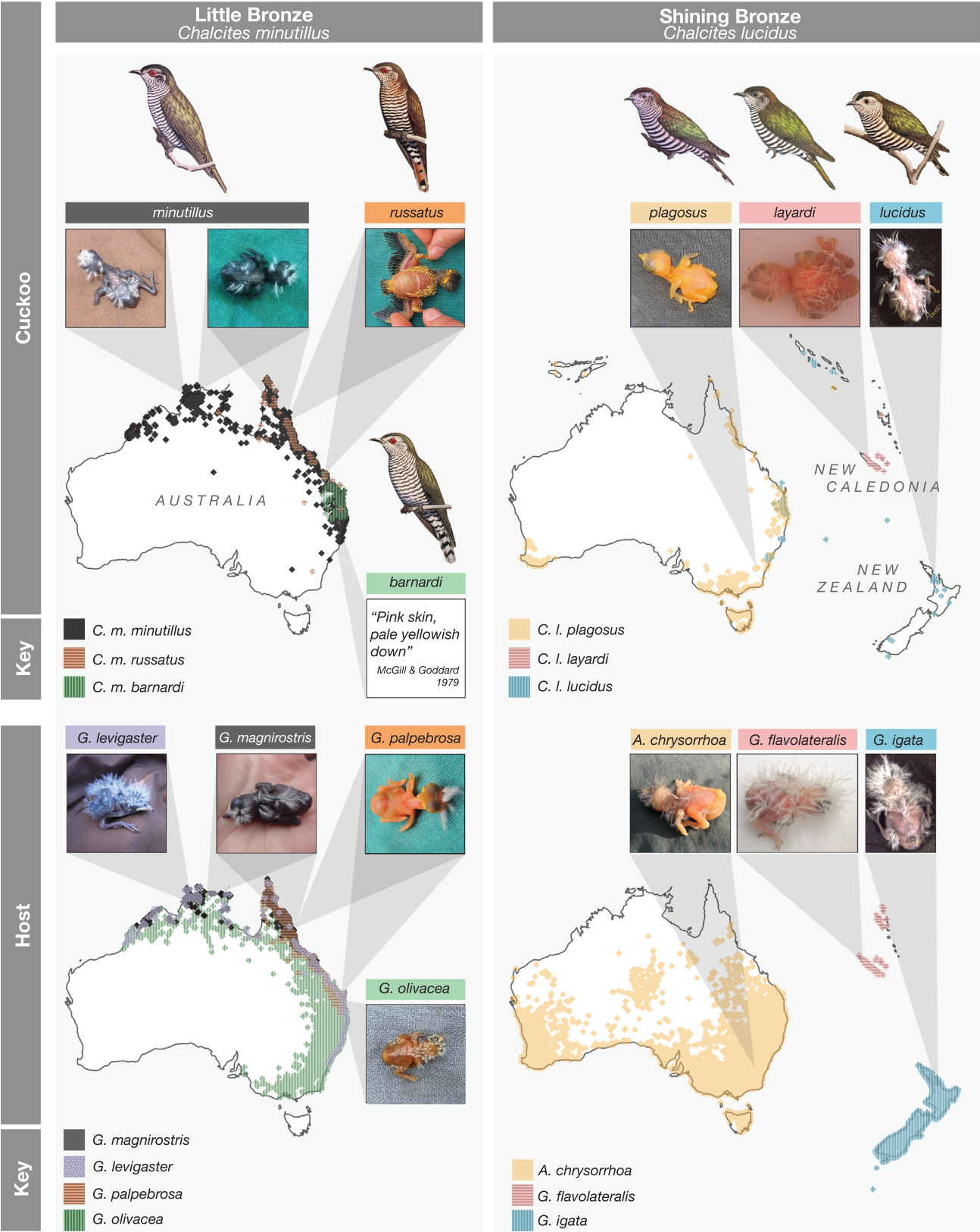
Fig. 4. Little bronze-cuckoo *C. minutillus* and shining bronze-cuckoo *C. lucidus* nestlings mimic the color of their respective host nestlings across their geographic range within Australia, New Caledonia, and New Zealand. Note that *C. lucidus lucidus* breeds only in New Zealand. Images: Adults are courtesy of J. Davies (*33*); nestlings *C. lucidus layardi* and *G. flavolateralis* are courtesy of A. Attisano, Polish Academy of Sciences (*12, 13*); *C. l. lucidus* and *G. igata* are courtesy of R. Thorogood, University of Helsinki, (*12, 13*); *G. olivacea* are courtesy of C. Taylor, University of Melbourne; other nestlings are courtesy of N.E.L. and H.-J.N. Description of *C. minutillus barnardi* nestlings from (*63*). The R v.4.0.3 package "ggplot2" was used to map subspecies distributions obtained from the Atlas of Living Australia (*64–66*) and eBird (*67*) (some islands were omitted for clarity).

morphs (fig. S9) indicate that genetic divergence driven by host preference is recent, ongoing, and does not yet constitute a complete reproductive barrier (Fixation Index $F_{ST} < 0.01$; table S2). Gene flow will reshuffle adaptive variation through recombination; as such, we may not observe genome-wide divergence during incipient speciation, especially at neutral or random loci, because adaptive variation may be restricted to a few key genes under selection. Assortative mating between different coevolutionary trait classes (i.e., individuals that produce black nestlings pair assortatively, as do individuals that produce pale nestlings) contributes to evidence that coevolving traits influence mating success (4).

What cues might facilitate assortative mating? Male and female cuckoos imprint on their host species and favor the breeding grounds of their host (41). Thus, *minutillus* individuals will favor the riverine habitat of large-billed gerygones, whereas *russatus* individuals will favor the rainforest-edge habitat of fairy gerygones. Such preliminary assortative mating may then be reinforced by premating isolation mechanisms such as vocalizations and plumage (42). These traits play vital roles in mate choice and species recognition in birds (43). We compared the calls of the *russatus* morph and the *minutillus* morph in sympatry and found that they differed subtly (20); calls of the *minutillus* morph were characterized by a significantly longer pause before the final note than that of the *russatus* morph (Fig. 3C). Similarly, male European cuckoo *Cuculus canorus* calls differed more between nearby populations that exploited different hosts than between distant populations that parasitized the same host (44). Plumage may also play a role in species recognition and mate choice (43), and the two morphs differ in some plumage traits (33) (Fig. 3C). Correlated evolution of coevolved traits (nestling skin color) and reproductive traits (calls or plumage) is suggestive of an influence of coevolving traits on mating success (4).

Coevolutionary diversification across the range of the brood parasites

Following this evidence of coevolutionary diversification in bronze-cuckoos, we would expect to find that subspecies of bronze-cuckoos will track divergent host nestling morphologies across their geographic range. This is indeed the case; nestling phenotypes of subspecies of the little bronze-cuckoo and the shining bronze-cuckoo in Australia, New Caledonia, and New Zealand (45) differ from one another in traits such as skin color, flange color, and the morphology of down feathers and bear a striking resemblance to the nestlings of their respective hosts (Fig. 4) (12, 13, 24, 46, 47). In contrast to the pronounced morphological differences between nestling bronze-cuckoos of different subspecies, the adults show only subtle plumage differences and all exhibit iridescent green dorsal plumage with barred white underparts (Fig. 4) (33). The correlation between a reproductive trait (plumage) and a coevolved trait (nestling skin color) across taxa contributes to evidence that coevolving traits influence mating success (4).

Discussion

We provide five sources of evidence of coevolutionary diversification in bronze-cuckoos at both macro- and microevolutionary scales (Fig. 1C and table S3) following the framework of Althoff *et al.* (4): (i) Current, ongoing coevolution; (ii) divergent selection on coevolving traits; (iii) coevolving traits influence mating success; (iv) selection limits gene flow among differentiated coevolved phenotypes; and (v) genetic or phenotypic diversification. Thus, we provide rare empirical evidence linking microevolutionary processes (i.e., processes driving genetic divergence between populations) with macroevolutionary patterns (i.e., speciation rates and processes) (3, 4).

Our study provides evidence that coevolutionary interactions between brood parasites and their hosts can drive speciation of the parasites, even in sympatry. This contrasts with a different mode of sympatric speciation that occurs in a less virulent brood parasite (27). In brood-parasitic *Vidua* finches, like bronze-cuckoos, nestlings show specialist mimicry of host young (48). However, unlike bronze-cuckoos, *Vidua* nestlings are reared alongside host nestlings and impose few costs on their hosts (49). Correspondingly, hosts have not evolved rejection of nonmimetic young (49). Instead, mimicry appears to have arisen through selection for nestling traits that exploit the preexisting provisioning rules of host parents (49, 50). Assortative mating occurs because both male and female *Vidua* finches imprint on their host (males mimic host songs and females use songs to choose a mate and a host nest to parasitize), providing a mechanism for reproductive isolation when a new host is colonized (27).

Our results, like those of the *Vidua* study (27), show speciation on only one side of the coevolutionary interaction, suggesting a process of speciation through host shift (51). However, the striking diversity of nestling morphologies among gerygones (Fig. 4)—in contrast to other nestling passerines, which are typically "uniformly drab" (52)—raises the possibility of cospeciation between bronze-cuckoos and their hosts. Mimicry of host nestlings by cuckoos may have selected for diversification of host nestling morphologies, as this would facilitate identification of parasite nestlings. Cospeciation between bronze-cuckoos and gerygones would be consistent with findings that gerygones have undergone more rapid and recent speciation than closely related taxa (53). Analogous diversification of host signatures has been documented in egg colors of brood parasite hosts (54) and cuticular hydrocarbon signatures of the ant *Formica fusca*, a host of socially parasitic ants (55).

Together, our results provide strong evidence that host defenses drive host specialization in highly virulent cuckoos, which in turn initiates speciation. An understanding of the processes of coevolutionary diversification is important, now more than ever, as anthropogenic climate change both disrupts existing tightly coupled interspecific relationships and generates new interactions (56). New parasite-host interactions could arise frequently and rapidly, accelerating rates of speciation. Understanding and modeling interspecies evolutionary dynamics will be critical for obtaining accurate models of environmental change and for prioritizing conservation efforts.

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SUPPLEMENTARY MATERIALS