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Patterns of coevolution in the adaptive radiation of crossbills

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Although evidence for coevolution and geographic variation in its apparent strength is increasing, we still have a relatively poor understanding of why coevolution varies among interactions. Here we review how variation in the occurrence of competitors, resource stability, habitat area, and time has affected the extent of trait escalation in coevolutionary arms races between crossbills (*Loxia*) and conifers. Competitors for conifer seeds, particularly tree squirrels, have limited the extent of crossbill–conifer coevolution; however, seed crop fluctuations reduce the extent to which tree squirrels limit crossbill–conifer coevolution. Crossbill densities increase with forest area, which results in greater escalation of seed defenses apparently as the result of stronger selection exerted by crossbills. The extent of trait escalation appears to increase toward lower latitudes where crossbill–conifer interactions have likely persisted locally for longer periods of time. However, because most crossbills occur at higher latitudes, much of the extant diversification of crossbills has occurred since the last glacial retreat, and the extent of trait escalation is limited. Nevertheless, coevolution has caused considerable trait evolution even in temperate regions. The conditions favoring coevolution between crossbills and conifers are widespread, and coevolution has played at least some role in at least three fourths of the taxa of crossbills.

Introduction

Coevolution, or the process by which reciprocal selection results in reciprocal adaptations among pairs or groups of interacting organisms, has been recognized as an important process affecting the organization and diversification of life since Darwin's time.[1–3] Recently, this view has gained support from two largely independent sets of studies. First, studies focusing on the geographic structure of contemporary interactions have repeatedly illustrated how geographically structured coevolution can drive adaptive divergence[4–12] (see Thompson[13] for review). With increasing frequency, empirical studies have demonstrated that the form of species interactions often, if not usually, varies across space, and that this can result in divergent selection favoring different phenotypes in different locales. Second, studies focusing on ecological speciation make a strong case that much of the diversity of life arises from divergent selection among populations.[14–17] If coevolution is a common driver of divergent selection between populations, and divergent selection is a major cause of speciation, then coevolution should play a large role in the diversification of life. However, we do not know how important coevolution has been in any adaptive radiation. Consequently, we need studies that quantify the importance and pervasiveness of coevolution across adaptive radiations. We also need studies that address the causes of variation in the extent and form of coevolutionary interactions so that we (1) understand why such variation arises and (2) can begin to predict conditions where
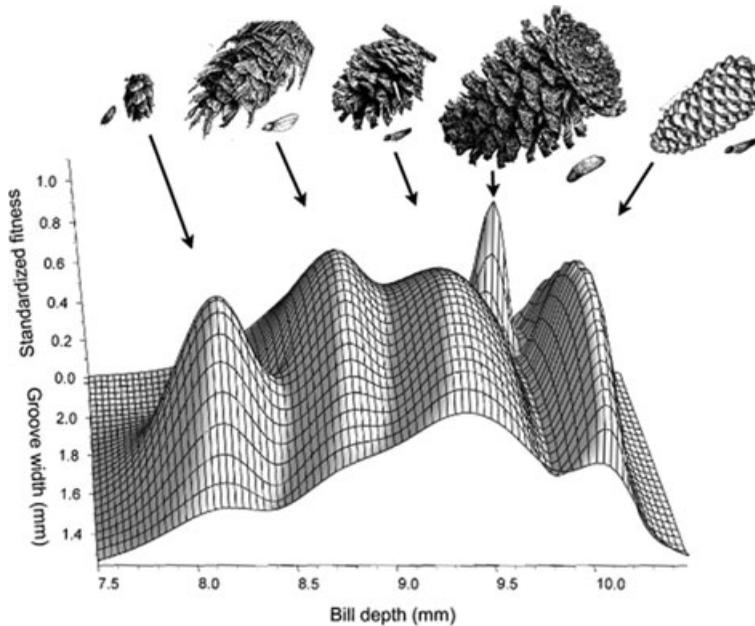
Figure 1. The estimated fitness for crossbills foraging on different species of conifers in western North America in relation to two key crossbill traits influencing feeding performance. The adaptive peaks for crossbills and the respective conifers from left to right: western hemlock, Douglas-fir, Rocky Mountain lodgepole pine where pine squirrels are present, Rocky Mountain ponderosa pine, and Rocky Mountain lodgepole pine in the South Hills where pine squirrels are absent, with cones and seeds drawn to relative scale (adapted from Benkman[30]). Crossbills experience divergent selection for foraging on the two forms of lodgepole pine as a result of coevolution in the absence of pine squirrels in the South Hills. The adaptive peak for foraging on Sitka spruce is not shown but likely occurs between the peaks for western hemlock and Douglas-fir.

coevolution will favor divergent selection between populations.

Here we review more than 10 years of research on the coevolutionary interactions between crossbills (Aves: *Loxia*) and conifers that has revealed how a wide range of both ecological and evolutionary factors influence the coevolutionary process and its potential to drive diversification. Crossbills are a highly specialized group of finches that have diversified to feed on seeds in the structurally diverse cones of different conifer species (Fig. 1).[18–20] In many cases, conifers have in turn evolved defenses against crossbills, and predator–prey coevolution has ensued.[5,6,9,10,19,21–24] These interactions have often been structured in a geographic mosaic of coevolution arising from spatial variation in a variety of ecological and evolutionary factors, and this variation has fueled diversification. Not only does this geographically structured coevolution cause divergent selection between populations of crossbills and conifers, but it also appears to be capable of causing ecological speciation in crossbills.[25] By focusing on

a broad spectrum of crossbill–conifer interactions characterized by a variety of ecological and evolutionary contexts, this research has shed light on the factors influencing variation in the coevolutionary process and the contribution of coevolution to the adaptive radiation of crossbills.

Crossbill foraging behavior, conifer seed defenses, and crossbill diversity

Crossbills and the conifers they specialize on are excellent subjects for studying the coevolutionary process because there is a clear functional link between phenotypes involved in reciprocal selection: the bill morphology of crossbills and the structure of the conifer cones upon which they feed. Crossbills forage in a stereotypic manner. They orient so that the vertical axis of the bill is aligned with the elongated surfaces of the cone scales and then bite between adjacent and often hard, woody scales. Their crossed and decurved mandibles are key because they enable crossbills to exert and withstand strong forces at the mandible tips (see Grant and Grant[26]).

If the mandibles were straight, the forces at the tips would be shearing, rather than compression forces, which would break the tips off. Once the mandible tips reach between adjacent cone scales, the lower mandible is abducted laterally, spreading the scales apart and exposing the seeds at their base.[20,27] After using their tongue to reach into the gap between the scales to lift the seed out, crossbills secure the seed in a lateral groove in the horny palate. Their lower mandible cracks the seed coat, and the tongue and lower mandible remove and discard the seed coat before the kernel is swallowed.

The main seed defense that crossbills must overcome is the structural defense provided by cone scales. Chemical defenses of conifer seeds appear relatively unimportant for crossbills except for the true firs (*Abies* spp.), where an abundance of resins probably explains why crossbills tend to avoid consuming many fir seeds at any one time even when they are readily accessible.[28] Conifer seeds have relatively thin seed coats presumably because conifers generally rely on the cone to deter predispersal seed predators. Consequently, crossbills have evolved large powerful bills to extract rather than husk seeds.[29] Bill depth in particular influences their ability to extract seeds from cones, while lateral groove width in the horny palate affects the speed at which seeds can be husked.[18]

Different taxa of crossbills have different combinations of bill depth and groove width, and most taxa studied to date appear to be specialized on a single species or subspecies of conifer (Fig. 1) that produces cones yearly and holds seeds in closed or partially closed cones through winter and spring.[9,18,27,30,31] These conifers represent key resources for crossbills because it is during winter and spring that food is most scarce, and presumably, selection is strongest.[18,31] For example, in the Pacific Northwest and Rocky Mountains, five conifers produce regular seed crops and hold seeds in their cones for an extended time.[18] Red crossbills are categorized into call or vocal types by their vocalizations, and call types differ in their bill and body sizes.[19,32–34] A different call type of red crossbill is adapted for foraging on each of these conifers: western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii menziesii*), Rocky Mountain lodgepole pine (*Pinus contorta latifolia*), and Rocky Mountain ponderosa pine (*P. ponderosa scopulo-*

rum)[5,18,30,35] (Fig. 1). Other conifers are foraged on, especially when crossbills move into regions without their key conifer, but each call type appears to be adapted almost like host races of insects to their respective key conifer.

Most of the conifer species specialized upon by crossbills evolved before the Pliocene[36] and well before the extant taxa of crossbills evolved,[37–39] thus cospeciation is unlikely common for crossbills and conifers. Nevertheless, coevolutionary arms races between crossbills and conifers have affected the evolution of both groups. Because crossbills forage as if to maximize feeding intake rates,[28,40] they avoid foraging on cones or trees whose seeds are difficult to access. This especially includes trees having thick cone scales that require greater forces to bite into and pry apart, preventing crossbills from accessing seeds quickly. Cone traits appear to be highly heritable in conifers,[41–45] and not surprisingly, thicker cone scales are the often-found evolutionary response to selection exerted by crossbills.[5,6,9,10,19,21,23,24,46,47] Although crossbills exert directional selection on conifers, they generally experience stabilizing selection when foraging on their key conifers[18,30,31] (Santisteban and Benkman, unpublished manuscript). Presumably the relatively short generation time of crossbills compared to conifers allows crossbills to adapt to the slower evolutionary changes in conifers.[6] The extent to which the coevolutionary arms race escalates is dependent on tradeoffs experienced by conifers that reduce the advantage of escalating seed defenses[6] and on the time available for coevolution to proceed. Later in the article we discuss the factors influencing the form and outcome of coevolutionary interactions between crossbills and conifers.

## Community context: presence and identity of preemptive competitors

Geographic variation in community context or composition is an important cause of variation in the form and outcome of many species interactions.[13,48] Many studies demonstrate that geographic variation in the occurrence and outcome of coevolution arises because of variation in the distribution of co-occurring species, including competitors,[11,49] alternative hosts,[50] and co-pollinators.[51,52] For example, the interaction between *Greya* moths and the *Lithophragma* plants they pollinate and oviposit on ranges from mutualistic to

antagonistic depending on the presence and abundance of co-pollinators.[51,52] Although an increasing number of studies implicate variation in community context as the cause of variation in the strength and form of species interactions, surprisingly few studies have provided a mechanistic or trait-centered understanding of such variation.[53] However, understanding the underlying mechanisms and traits involved at the phenotypic interface of the interactions[53–55] is crucial to understand the causes and consequences of geographic variation in the structure of species interactions and the general importance of coevolutionary interactions.

Studies of crossbills and Rocky Mountain lodgepole pine in areas with and without pine squirrels (*Tamiasciurus* spp.) (Fig. 2) provide such a trait-centered understanding of coevolution. The contrast in crossbill–conifer interactions between areas with and without pine squirrels is particularly striking because pine squirrels are voracious preemptive competitors for seeds in lodgepole pine cones that depress the abundance of crossbills throughout most of the Rocky Mountains.[19,56] Here, pine squirrels drive cone evolution and crossbills adapt to cones that are relatively poorly defended against crossbills.[5] However, in some isolated mountain ranges east and west of the northern Rocky Mountains, pine squirrels are absent and crossbills are up to 20 times more abundant than in areas with pine squirrels. Pine squirrels have not colonized these isolated mountain ranges such as the South Hills of Idaho (Fig. 2) because they do not traverse the large intervening treeless plains. In the absence of pine squirrels, seed defenses have evolved in response to selection exerted by crossbills (12% increase in scale thickness; Table 1).[5,6,19] The increase in seed defenses has favored an increase in bill size leading to strong divergent selection on crossbills between areas with and without squirrels (Fig. 1).[6,30] Bill depth is highly heritable in crossbills,[34] and thus divergent selection has caused local adaptation and predator–prey coevolution has ensued. Crossbills have diverged in both bill morphology and flight calls here, which has led to high levels of reproductive isolation between the endemic crossbills in the South Hills (*Loxia sinesciurus*) and other call types of red crossbills (*Loxia curvirostra* complex) that visit the South Hills yearly.[25,57] Other studies relating comparisons between areas with and without pine squirrels involving black spruce (*Picea*

mariana[9]) and Douglas-fir (Table 1) further indicate that conifers have evolved in response to elevated selection exerted by crossbills in the absence of pine squirrels. In the case of black spruce, crossbills have also adapted to the increased defenses where pine squirrels were historically absent on Newfoundland and the coevolutionary changes are strikingly convergent with those found in lodgepole pine.[9]

Tree squirrels in the genus *Sciurus* also harvest cones before they open. However, *Sciurus* harvest many fewer cones than do *Tamiasciurus*,[58] which reduces the competitive and presumably selective impacts of *Sciurus* as compared to *Tamiasciurus*. Evidence indicating that *Tamiasciurus* have had a stronger evolutionary impact on conifers than have *Sciurus* includes variation in levels of seed defense directed at tree squirrels. An overall measure of seed defense directed at tree squirrels is the ratio of cone mass to seed mass (cone mass or defense per seed).[5,21,59] Tree squirrels tend to preferentially forage on trees whose cones have lower cone mass to seed mass ratios, and this ratio decreases in the absence of tree squirrels presumably owing to the relaxation of selection exerted by them. However, this increase is greater (Welch's ANOVA, $F_{1,3.32} = 9.73$, $P = 0.046$) in the absence of *Tamiasciurus* (18.4–63.8% for lodgepole pine, black spruce, Douglas-fir, and western hemlock) than in the absence of *Sciurus* (0.6–5.4% for Aleppo pine *P. halepensis* and ponderosa pine *P. ponderosa*; Table 1). Further suggestive of a stronger evolutionary impact by *Tamiasciurus* than by *Sciurus* is geographic variation in cone ripening phenologies. In particular, pine and spruce with nonserotinous cones (serotinous cones remain closed and hold their seeds for several or more years until heated by fire) within the range of *Tamiasciurus* (North America north of Mexico) tend to produce cones that begin to open within several weeks after seeds mature, minimizing the window of time that *Tamiasciurus* can cache cones. Outside the range of *Tamiasciurus* but within the range of *Sciurus* (e.g., Mexico, Eurasia), the seeds of pine and spruce tend to mature at about the same time as in North America, but many species have cones that remain closed through winter.[20,60] Because larger bills are favored for foraging on closed than on open cones of a given conifer species,[18] these differences in cone-ripening phenologies likely account for the larger bill sizes of crossbills in Mexico, Central America, and the Old
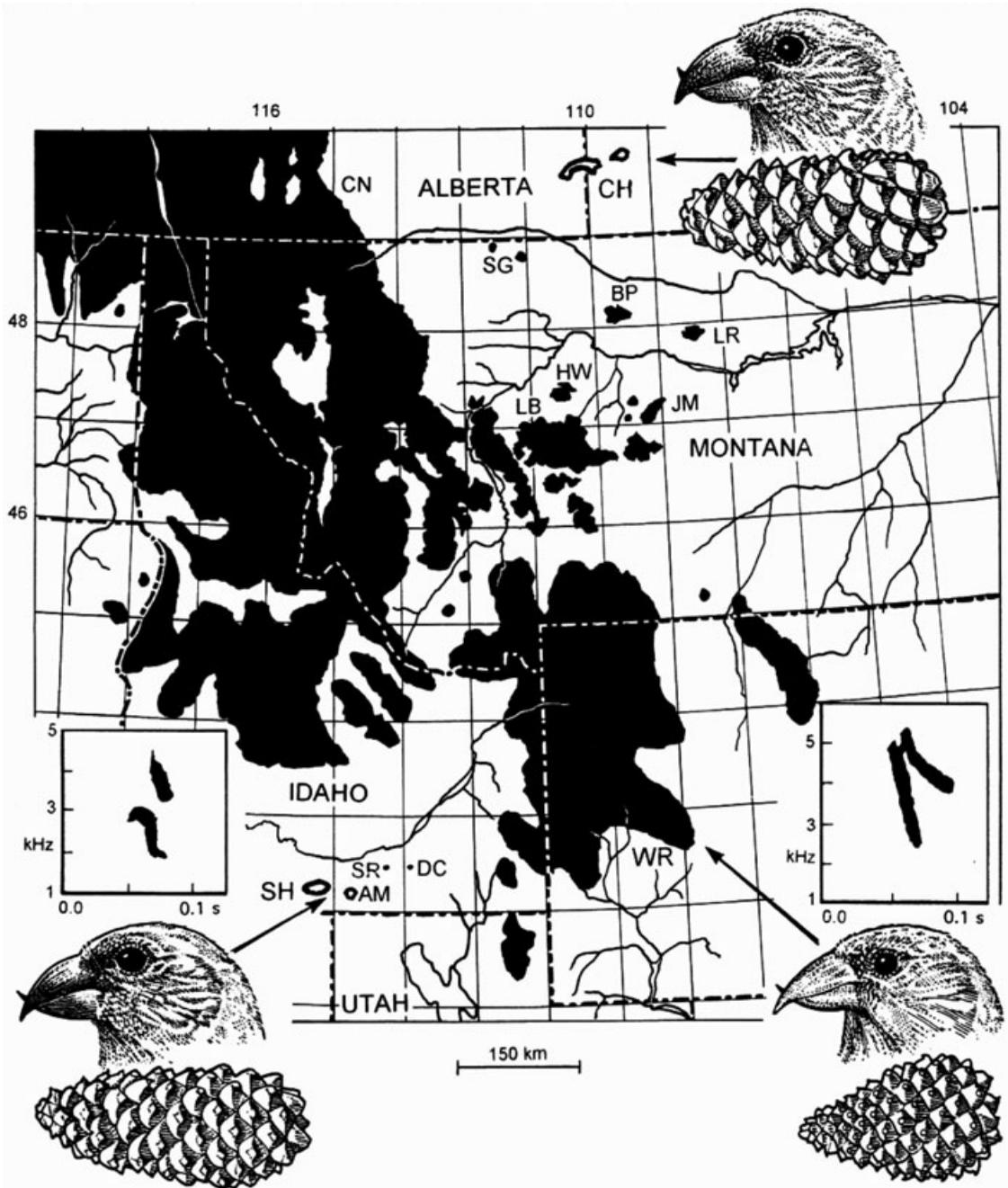
Figure 2. The distribution of Rocky Mountain lodgepole pine (black) and crossbills and cones in the Rocky Mountains (lower right), Cypress Hills (upper right), and South Hills and Albion Mountains (lower left). Representative sonograms of flight calls are shown for the South Hills crossbill (lower left) and the Rocky Mountain lodgepole pine crossbill (lower right). *Tamiasciurus* pine squirrels are found throughout the range of lodgepole pine, except in some isolated mountains, including the Cypress Hills (CH), Sweetgrass Hills (SG), Bears Paw Mountains (BP), Little Rocky Mountains (LR), South Hills (SH), and Albion Mountains (AM). Pine squirrels were absent from the Cypress Hills until they were introduced in 1950 (from Benkman[19]).

Table 1. Distal cone scale thickness and percentage increase in scale thickness between areas where crossbills are common (no tree squirrels) relative to areas where crossbills are uncommon or absent (tree squirrels present or area of forest is small)

Conifer	Scale thickness (mm)		Percent increase in scale thickness in areas where crossbills are more common	Cone mass/seed mass		Percent decrease in cone mass/ seed mass in absence of tree squirrels
	Crossbills common	Crossbills uncommon		Squirrels present	Squirrels absent	
Stable seed availability						
Lodgepole pine	2.90	2.59	12	85.11	30.77	63.8
Black spruce	1.18	1.02	15	54.05	36.23	33.0
Aleppo pine	3.14	2.83	11	17.65	17.54	0.6
Fluctuating seed availability						
Douglas-fir	1.21	1.16	4	18.72	13.98	25.3
Western hemlock	0.68	0.68	0	24.48	19.96	18.4
Ponderosa pine	5.80	5.13	13	13.95	13.20	5.4
Black pine	3.65	3.06	19			
Mountain pine	6.56	5.28	24			
Hispaniolan pine	3.66	2.38	53			

World than in North America (see Griscom[61]). Alternatively or in addition, the weaker competition between crossbills and *Sciurus* (even in areas where cones remain closed for extended periods, *Sciurus* do not harvest the quantities of cones that *Tamiasciurus* harvest) may allow crossbills to have a consistently greater selective impact in regions where *Tamiasciurus* are absent, favoring greater crossbill defenses, and thus larger bills as a result of stronger coevolution between crossbills and conifers.

One highly specialized *Sciurus*, however, has a large impact on the crossbill–conifer interaction.[10] Abert's squirrels (*S. aberti*) are highly dependent on Rocky Mountain ponderosa pine (*P. ponderosa scopulorum*) and limit seed available to crossbills not only because of direct seed predation but especially because Abert's squirrels are specialized for feeding on the inner bark of twigs. They depress seed abundance by biting off branches for inner bark feeding, which terminates the development of vast numbers of cones months before seeds mature (Parchman and Benkman[10] and references therein). In areas where Abert's squirrels are absent, ponderosa pine has evolved thicker scales as a defense against crossbills (Table 1) presumably because crossbills are stronger selective agents. Other evidence that the presence and absence of *Sciurus* affects the interac-

tions between crossbills and conifers is less consistent (e.g., Benkman and Parchman[21]) than for the examples concerning the presence and absence of *Tamiasciurus*.

Resource stability

Above we reviewed evidence that the strength of competition influences the extent of coevolution between crossbills and conifers. Now it is logical that we discuss the factors that affect the strength of competition. In this section we address temporal variation in resource stability because it is thought to have an impact on competition and appears in our work to influence the coevolutionary process. Although Wiens[62] argued that competition is less important when environments are variable, subsequent empirical (e.g., Grant[63]) and theoretical (e.g., Chesson and Huntley[64]) studies indicate that fluctuating environments or resources do not necessarily restrict competition. Later we describe the situation for crossbills and tree squirrels when cone crops are stable from year to year and then contrast this to the situation when cone crops fluctuate annually.

One of the reasons coevolution was so easily detected between crossbills and lodgepole pine was that its cone crops are extremely stable from year to year and crossbills forage on seeds that have
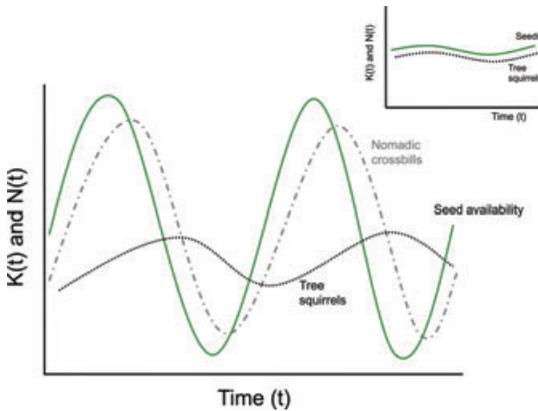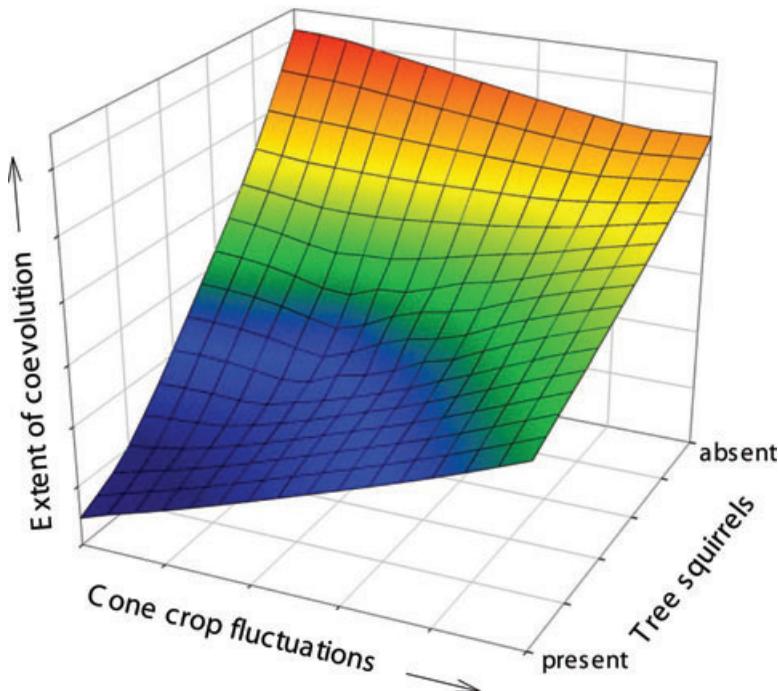
Figure 3. A schematic illustrating the relative extent to which crossbills and tree squirrels track annual fluctuations in seed resources (after May[106]). Sedentary tree squirrels are unable to track large annual fluctuations in cone (seed) crops, whereas nomadic crossbills excel at tracking regional fluctuations in cone crops. With little annual variation in seed availability, tree squirrels are able to track and deplete a greater proportion of the cone crop (inset in upper right) and are thus much stronger seed competitors preventing crossbills from having much of an evolutionary impact on conifers.

remained for years and even decades in closed cones[6] (most lodgepole pine trees in the absence of tree squirrels produce serotinous cones[65]). The result is that crossbills can be sedentary and thus adapt and coevolve with local populations of lodgepole pine.[6,57] Another consequence is that sedentary competitors such as *Tamiasciurus* can achieve high population densities and serve as strong selective agents and preemptive competitors, further giving rise to strong geographic variation in the form and outcome of selection on cone and bill traits.[5,6,9] Such reliable seed supplies also characterize black spruce[9] and Aleppo pine.[24] Cone scales have increased in thickness to a strikingly similar extent (11–15%) for these three species of conifers (Table 1) in areas where crossbills are common (squirrels are absent) relative to areas where they are less common; crossbills are less common because either tree squirrels are present (e.g., lodgepole pine, black spruce) or forest areas are small and isolated (e.g., Aleppo pine). However, local and even regional seed availability varies tremendously from year to year[66,67] in most other conifers that crossbills rely upon. This favors crossbills that can track such fluctuations (Fig. 3) and explains the extreme nomadic tendencies of most crossbills.[20,28,66,68,69] In contrast, the relatively sedentary tree squirrels are

less able to track such cone crop fluctuations and therefore consume a relatively small percentage of the seeds during large cone crops (Fig. 3).[70,71]

Because crossbills can track regional fluctuations in seed crops whereas tree squirrels cannot (Fig. 3), crossbills should have a greater impact on cone evolution in the presence of tree squirrels when cone crops fluctuate than when they are stable (Fig. 4). Consequently, the differences in the extent of coevolution between crossbills and conifers in areas with and without tree squirrels should be less when cone crops fluctuate than when they are more stable (Fig. 4). This prediction is supported by comparisons of Douglas-fir cones from the San Juan Islands where pine squirrels are absent to those in the Cascade and Olympic mountains where pine squirrels (*Tamiasciurus douglasii*) are present. On the San Juan Islands, Douglas-fir has reduced pine squirrel defenses (e.g., a 25.3% decrease in cone mass to seed mass ratio relative to the mainland: Table 1; $F_{1,115} = 59.46$, $P < 0.0001$) while cone scales are 4% thicker (Table 1; $F_{1,115} = 6.29$, $P < 0.0135$) implying an increase in crossbill defenses. The smaller increase in scale thickness relative to other more stable conifers (Table 1) could reflect less of an evolutionary effect by crossbills on conifers when cone crops fluctuate. However, the large difference in scale thickness in ponderosa pine between areas with and without Abert's squirrels (*Sciurus*) described earlier (Table 1) suggests that cone crop fluctuations per se do not limit the ability of crossbills to exert strong selection. Instead, the smaller increase in Douglas-fir cone scale thickness in the absence relative to the presence of pine squirrels is perhaps more likely the result of greater coevolution between crossbills and conifers in the presence of tree squirrels (Fig. 4).

Western hemlock is another conifer with cone crops that fluctuate and is specialized upon by a call type of red crossbill (call type 3).[18] We compared western hemlock cones from the Queen Charlotte Islands where pine squirrels were absent, until recent introductions, and crossbills are common[72] to those from coastal British Columbia and southeast Alaska where pine squirrels occur. Although we detected evidence of a loss of pine squirrel defenses in the absence of pine squirrels on the Queen Charlotte Islands relative to the mainland (e.g., an 18.4% decrease in cone mass to seed mass ratio; $F_{1,219} = 13.06$, $P = 0.0004$; Table 1), we did not

Figure 4. A schematic illustrating how the extent of coevolution between crossbills and conifers varies in relation to variation in cone crop fluctuations and the presence and absence of tree squirrels. The presence of tree squirrels has its greatest impact when cone crops are stable (Fig. 3). Most conifers relied upon by crossbills produce variable cone crops, therefore coevolution should occur frequently between crossbills and conifers.

detect an increase in scale thickness ($F_{1,219} = 0.02$, $P = 0.90$). However, this should not be surprising because hemlock cone scales are so thin and pliable (Fig. 1) and provide relatively little defense against crossbills, and thus slight variation in scale thickness is unlikely to have an impact on crossbills (Table 1; black spruce cone scales are also relatively thin, but they are rigid and require large forces to spread apart[9]). Alternatively, we might expect increases in defenses related to handling seeds rather than seed extraction for western hemlock, because crossbills spend about twice as much time handling seeds relative to removing them from hemlock cones than, for example, from Douglas-fir cones.[18] Indeed, seed coat mass was 24.6% heavier in the absence of pine squirrels than in their presence (ANCOVA: $F = 32.2$, df = 1, $P < 0.0001$ for effect of squirrel presence–absence on seed coat mass; $F = 0.01$, df = 1, $P = 0.47$ for effect of kernel mass; $F = 0.01$, df = 1, $P = 0.48$ for squirrel presence–absence × kernel mass interaction). This suggests that western hemlock has increased its defenses directed at crossbills in the absence of pine squirrels.

Although our data indicate that conifers producing variable seed crops evolve in response to selection exerted by crossbills (and tree squirrels), we have less evidence for reciprocal adaptation by crossbills to geographic variation in cone and seed traits of conifers with fluctuating cone crops (compared to those specialized on conifers that do not produce fluctuating cone crops). There are two reasons for this. First, divergent selection on crossbills between areas with and without tree squirrels should be less for most fluctuating conifers than for more stable seed producers (Fig. 4). Local adaptation is more likely when divergent selection is stronger (e.g., Galen *et al.*[73]). Second, crossbills are nomadic when cone crops fluctuate, which increases the potential for gene flow to swamp local adaptation (e.g., Hendry *et al.*[74]) and therefore local adaptation is unlikely unless the areas with and without tree squirrels are each large enough to continuously support populations of crossbills. Because habitat area is an important source of variation affecting the coevolutionary interactions between crossbills and conifers, we discuss it in the next section.

Habitat area and the strength and form of selection

Habitat area affects the occurrence, abundance, and evolution of species.[75–78] Consequently, we expect that when habitat area varies among regions, the strength and form of species interactions and the extent of coevolution would also vary. We have found such evidence in crossbills and conifers as forest area varies in size. For example, crossbill population density increases logarithmically with increases in the size of isolated forest islands (tree squirrels absent) of lodgepole pine east and west of the Rocky Mountains.[56] Variation in crossbill density appears to influence the strength of selection crossbills exert as shown by the increase in seed defenses that deter crossbills with increases in crossbill densities.[56] Furthermore, the average bill size of crossbills in these forest islands increases with seed defenses, which indicates that the extent of coevolution and divergent selection it generates varies with forest area.[56]

Black pine (*Pinus nigra*) cone crops are more variable from year to year than those of lodgepole pine, and all or nearly all black pine seeds are shed from the cones by late spring.[79] Crossbills therefore are presumably nomadic when alternative seed resources are not consistently available. Nevertheless, the extent of apparent seed defenses directed at crossbills in continental areas of the eastern Mediterranean (tree squirrels present) increases with the area of black pine forest with smaller more isolated areas having the lowest levels of crossbill defense.[21] Larger less isolated forests should be easier for nomadic crossbills to locate and are more likely to allow crossbills to persist at higher densities and exert stronger selection. Similarly, the level of seed defenses directed at crossbills in the extensive forests of mountain pine (*Pinus uncinata*) in the Pyrenees is much greater than in small isolated stands of mountain pine in south central Spain (Table 1).[23] In the small isolated stands, seed predation by crossbills is lower and more variable from year to year likely reflecting crossbill populations that are more transitory than those in the Pyrenees[23] (see also Clouet and Joachim[46]). Crossbills are resident in mountain pine forests in the Pyrenees,[79] and these crossbills have significantly deeper bills than those in other pine forests 10–50 km away[81] implying local adaptation and coevolution between crossbills and mountain pine.[23] In sum, larger forests support higher densities of crossbills, conifers in these forests show enhanced defenses directed at crossbills, and in some cases, we find evidence of reciprocal adaptation in crossbills. We predict that variation in habitat patch size will commonly alter the strength and form of species interactions by altering both the abundance and distribution of species and thereby be an important factor shaping the geographic mosaic of coevolution. In addition, variation in population size, as a result of variation in habitat area, may affect rates of molecular evolution, with rates increasing as population size increases.[78]

Optimal prey size and the form of selection

All predators that secure and process prey individually likely have an optimal prey size or optimal range of prey sizes. At one extreme, relatively small prey provide too little reward to the predator for the effort to secure and process the prey item. At the other extreme, large prey may be too difficult to secure or process for the rewards; handling costs tend to accelerate with increasing prey size.[29,82] The optimal cone size for *Sciurus* appears to occur in the range of 60- to 80-mm-long cones.[10,24] When cones are smaller than this threshold, *Sciurus* prefer to forage on larger cones. When cones are larger, *Sciurus* prefer smaller cones. *Tamiasciurus* likely behave similarly. Consequently, when cones are small (<60 mm long) they evolve to even smaller sizes in the presence of tree squirrels (e.g., lodgepole pine,[5,19] black spruce,[9] Douglas-fir and western hemlock [Parchman and Benkman, unpublished data]). When cones are large (>80 mm long) they evolve to even larger sizes in the presence of selection exerted by tree squirrels (e.g., Aleppo pine,[24] ponderosa pine *P. p. ponderosa*[10]). This in turn determines how crossbills are affected by the presence of tree squirrels because crossbills prefer and forage more efficiently on smaller cones with thinner scales.[6,10,19,21,83] For a conifer producing smaller cones, the negative effect of tree squirrels on crossbills is mostly competitive—a density-mediated indirect effect—because selection exerted by tree squirrels favoring smaller cones does not hinder crossbills.[19] In contrast, when conifers produce larger cones the negative effect of tree squirrels on crossbills is primarily evolutionary where the increase in cone size as a result of selection exerted by tree squirrels can lead to cones that are too difficult for crossbills to forage upon efficiently—a

trait-mediated indirect effect. This prevents crossbills from accessing the resource as effectively as when tree squirrels preemptively harvest cones. For example, ponderosa pine in the Sierra Nevada has evolved very large cones in response to selection exerted by *Sciurus griseus*, and as a consequence, crossbills largely avoid ponderosa pine in this area.[10] The important question then is why initially cones vary in size among conifers.

Cone size is correlated with seed size. For example, cone length of 25 species of North American pines is positively correlated with seed mass (not controlling for phylogeny, $r = 0.91$, $P < 0.0001$; data from McCune[84]), excluding wingless-seeded pines that tend to occupy habitats where tree squirrels are absent[85] and pine species whose seeds exceed 300 mg. Notably, the wingless-seeded pines, which consistently occur in the absence of tree squirrels, have relatively small cones. What causes seed size variation is less clear. We have not detected correlations between abiotic factors and seed size[5,23] nor have we found seed predators to exert selection in a consistent manner on seed size.[6,10,11,21] One biotic factor that may contribute to seed size variation is herbivory on seedlings. Because seedlings growing from larger seeds may be able to allocate more resources to defense than seedlings growing from smaller seeds,[86] seed size variation among locations could be related to variation in herbivory on seedlings (J. P. Bryant, personal communications). It is fascinating to think that variation in herbivore pressure on seedlings may influence whether the dominant interaction between tree squirrels and crossbills is exploitative competition or the consequence of an evolutionary effect by tree squirrels on the conifers. An interesting hypothesis here is that the latitudinal gradient in seed size (increasing seed size toward the tropics[87]) is related to the increasing intensity of species interactions (e.g., herbivory at lower latitudes[88] but see Adams and Zhang[89]).

Interaction time and extent of coevolution

Coevolution is different from adaptation to the abiotic environment because the genetic feedback of coevolution results in continuously changing optimum phenotypes.[13,88] Escalation of the crossbill–conifer coevolutionary interaction is expected because crossbills consistently exert directional selection on conifers by preferentially foraging on less-defended cones and favoring increased scale thickness. The considerably shorter generation time of crossbills than conifers allows crossbills to adapt to and track the evolutionary changes in the conifers, and to potentially exert similar levels of selection over time. Whether the extent to which the coevolutionary arms race escalates is dependent on time for coevolution to proceed or on tradeoffs experienced by conifers reducing the advantage of escalating seed defenses[6] can be addressed by comparing the extent of trait escalation in relation to the time intervals available for coevolution. Here we focus on scale thickness rather than the bill size of crossbills because suitable crossbill comparisons simply do not exist in some cases (e.g., we have estimates of bill size in only one of the two regions for Hispaniolan pine [*Pinus occidentalis*], and Aleppo and mountain pine). However, inferring changes in bill depth in response to evolutionary changes in scale thickness is reasonable given that bill depth tends to match cone structure[9,18,21,23,30,56] and that relatively large-billed crossbills are associated with conifers that have evolved enhanced scale thickness in apparent response to selection exerted by crossbills.[5,6,9,19,21–24,47]

Crossbills and some conifers have coevolved only recently[5,9] whereas others have likely coevolved for much longer.[47] For example, black spruce, but not pine squirrels, colonized Newfoundland around 9,000 years ago after the ice retreated and crossbills and black spruce have apparently coevolved there since.[9] Similarly, crossbills and lodgepole pine in the South Hills have likely coevolved for only 5,000–7,000 years.[5] Scale thickness has increased in these two conifers 15% and 12%, respectively, as a result of coevolutionary arms races (Table 1). We assume that the increases in scale thickness in other North Temperate conifers such as Douglas-fir and ponderosa pine are similarly the result of coevolution over time periods less than 10,000 years, as the distribution of these conifers also changed dramatically after the last glacial retreat.[10,18] At the other extreme, crossbills and pine have likely been coevolving on Hispaniola for up to 550,000 years.[47] Given that crossbills and pine have coevolved for so much longer on Hispaniola than in other crossbill–conifer systems it is not surprising that scale thickness has increased so much in Hispaniolan pine (53%) relative to the conifers in other systems (Table 1). This suggests that the longer the time interval allowed for

predator–prey coevolution, the more pronounced the phenotypic evolution and divergence.

Aleppo pine is a Mediterranean species whose level of increase in scale thickness on Mallorca is comparable to North Temperate conifers (Table 1). As in lodgepole pine and black spruce, we suspect that crossbills and Aleppo pine have been coevolving on Mallorca for less than 11,000 years following the colonization by Aleppo pine from putative Pleistocene refugia in northeast and southeast Spain.[90,91] In contrast, two other pines in the Mediterranean, mountain and black pine, display relatively large increases in cone scale thickness (Table 1) implying either longer time intervals for coevolution or fewer tradeoffs than for other temperate conifers. Mountain pine likely covered similar total areas on the Iberian Peninsula including the Pyrenees over the last 20,000 years or more.[92] Consequently, the elevated levels of defense in the Pyrenees are likely related to coevolution occurring over tens of thousands of years. We do not know how long black pine and crossbills have been coevolving on Cyprus (Table 1), but we suspect that it has also been occurring for well over 10,000 years because Pleistocene glaciations had less of an effect on plant distributions in the eastern than western Mediterranean,[93] and black pine could have moved to lower elevations in Cyprus during the last glacial retreat.

In sum, the variation in the evolution of crossbill defenses in conifers (Table 1) is influenced by the temporal duration of crossbill–conifer coevolution. Greater increases in scale thickness are associated with longer periods of time over which coevolution has likely proceeded. However, time is not the only variable differing among the interactions. For example, selection from tree squirrels might also contribute to this variation, and some comparisons contrast areas with and without tree squirrels (e.g., lodgepole pine, black spruce, ponderosa pine) whereas other comparisons are between areas with tree squirrels either absent from both (e.g., Aleppo, black, and Hispaniolan pine) or tree squirrels are uncommon in both (mountain pine). In spite of this additional variation, comparisons involving crossbill–conifer systems where there are endemic crossbills (lodgepole, Aleppo, black, mountain and Hispaniolan pine, and black spruce) indicate that the extent to which cone scales have increased in thickness appears approximately related to the length of time the interaction has occurred.

What role tradeoffs experienced by conifers plays is unknown. However, given the tremendous diversity of cone structures among pines (e.g., Perry[60]), we suspect that tradeoffs have had a minimal impact in limiting the response of conifers to selection exerted by crossbills.

Coevolution in the adaptive radiation of crossbills

Although crossbills probably diverged from redpoll-like (*Carduelis* sp.) ancestors about 6 million years ago,[94] much of the diversification of extant red/common crossbills (*L. curvirostra* complex) in North America and in the Old World has been recent.[38,39,95] This diversification presumably coincides with the expansion of conifer forests during the last 11,000 years after the last glacial retreat. We suspect that crossbills have undergone repeated radiations when conifer distributions expanded during the 21 interglacial periods of the Pleistocene (about 2.6 million years),[96] alternating with equally extensive crossbill extinctions coinciding with the contraction of conifer forests following glacial advances.[97] Consequently, most, and especially the more northern, crossbills have had a limited time for coevolutionary interactions to cause much evolutionary divergence. Nevertheless, the levels of morphological divergence in crossbills that have arisen in the last 11,000 years or less because of coevolutionary arms races are substantial. For example, the South Hill crossbill has a bill depth over 6% deeper than in the other crossbill specialized on lodgepole pine (call type 5), where coevolutionary interactions are much weaker (Fig. 2). A 6% increase is substantial given that many different call types of crossbills differ by only 2% or 3%,[32,33] and these differences lead to substantial variation in feeding rates.[18,30] Indeed, some of the differences in bill size between crossbills specialized on different populations of the same species of conifers (e.g., black spruce and lodgepole pine) are much greater than those between crossbills specialized on different species and even genera of conifers.

These studies suggest that coevolution has been a prominent force in the evolution of crossbills throughout the last 6 million years. Only for crossbills specialized on conifers that produce stable seed crops and where tree squirrels, especially pine squirrels (*Tamiasciurus*), are important seed predators, do we expect coevolution between crossbills and

conifers to be relatively unimportant (Fig. 4). This represents a minority of crossbills. Our studies on eight New World crossbills suggest that coevolution has been important for six of them. We suspect coevolution has also been an important process for the crossbill in Central America (*L. c. mesamericana*; cone scales of *P. caribaea hondurensis* in Central America are thicker than those of *P. c. bahamensis* where crossbills are absent[98]) and even the Mexican crossbill (*L. c. stricklandi*) although we do not have suitable comparisons for the latter taxon. This suggests that over three fourths of the New World crossbills are actively engaged in coevolutionary arms races. Such a high prevalence is not surprising given the widespread conditions favoring coevolution, and in sum indicate that coevolution has been a prominent source of divergent selection underlying the adaptive radiation of crossbills.

Synthesis and future directions

Our two main conclusions are that coevolution is an important process contributing to the diversification of crossbills and conifers and that the extent of trait escalation and outcome of coevolution varies because of the presence and absence of competitors and spatial and temporal patterns of resource availability. Specialized species such as crossbills that interact strongly with other species are expected to evolve defenses and counter-offenses (i.e., coevolved traits) and show some degree of local adaptation.[3] Thus, widespread evidence for coevolution between crossbills and conifers is not surprising. However, such evidence is not trivial because we do not know of comparable evidence for any other adaptive radiation. In addition, our results also suggest when specialized species do not coevolve. Namely, coevolution is prevented when competitors keep specialist species uncommon so that they exert relatively weak if any selection on their prey.

Geographic variation in the form and outcome of coevolutionary interactions is not unique to crossbills. An increasing number of studies provide evidence of such geographic variation.[13] These studies include those on moths (*Greya*) and the plants (*Lithophragma*) they pollinate and oviposit in,[51,52] flies (*Prosoeca*) and the plants (*Zaluzianskya*) they pollinate,[4] webworms and the plants they feed upon,[50] weevils (*Curculio*) and the camellia fruits (*Camellia*) they feed upon,[12] and garter snakes

(*Thamnophis*) preying on toxic newts (*Taricha*).[7,8] These studies indicate that geographic variation in both species interactions and the extent of coevolution is a widespread phenomenon. Although such studies demonstrate that geographic variation in the form and outcome of the coevolutionary process is an important aspect and generator of diversity, most have provided limited insight into the underlying causes of geographic variation in species interactions (other than distributional differences; see Craig *et al.*[49]). This in turn limits our ability to understand why such geographic variation arises.

The strength of our studies on crossbill–conifer interactions is an understanding of the causes of geographic variation in both the species interactions and the extent of coevolution, and these causes are likely general to many systems. Geographic variation in community context (e.g., the occurrence and abundance of a superior competitor) for crossbills and conifers has caused variation in the strength of coevolution and thereby drives divergent selection between many populations of crossbills and conifers. This variation in community context arises from a variety of factors, including barriers to dispersal (e.g., nonforested habitats or water) that differentially affect the colonization of habitats by different species and variation in habitat area that differentially affect the occurrence and abundance of species. Interacting species commonly differ in their ability to cross barriers, thus variation in community context is expected to be common where barriers divide habitats. Many species vary in abundance as habitat patch size varies[75] and different species have different patch size thresholds below which they do not persist.[76] Consequently, variation in habitat area or patch size is widespread and likely to influence both the strength of interactions and the extent to which many species interact with the same set of species throughout their ranges. Regional differences in resource variability could also act to influence the strength of species interactions. These are all important factors for ecologists studying communities and species interactions, and we believe that those interested in coevolution and the factors underlying geographic variation in the process would benefit from considering these factors. Our studies also highlight how the coevolutionary process can cause geographic isolation to be a powerful force in speciation.[25]

Finally, the extent of coevolution and geographic differentiation has increased with time. The longer the time interval crossbill–conifer interactions have persisted, the greater the apparent escalation in the arms race. One result is that the extent of coevolution increases toward lower latitudes where conifer (and presumably crossbill) distributions have been more stable and interactions have persisted longer. Notably, crossbills in the Old World that occur farthest south with black pine, Aleppo pine and *Pinus kesiya* (*L. c. guillemardi*, *L. c. poliogyna*, and *L. c. meridionalis*, respectively), and in forests that were likely present during the last glacial retreat, have the largest bills among crossbills associated with these conifers. Similarly, in the New World, the greatest increases in scale thickness occur in subtropical Hispaniola,[47] where pines have likely persisted for even longer. Our evidence for the extent of trait escalation increasing with time and our evidence for very strong interactions (i.e., extent of evolutionary changes) in temperate latitudes (e.g., Refs. 5,6,9; see Bryant *et al.*[99] for an example from even higher latitudes) suggest that the escalation of trait values toward lower latitudes[12,100] is the result of the interaction persistence rather than the strength of the interactions being inherently stronger at lower latitudes. In this regards, our findings contrast with the view of Dobzhansky[101] and Schemske[88,102] who emphasize that stronger species interactions are likely to underlie the latitudinal biodiversity gradient. Nonetheless, our results are consistent with the idea that the latitudinal variation in species interactions and coevolution has been important in shaping the latitudinal biodiversity gradient. A large role is especially likely if the causes of geographic variation in community context we described earlier are magnified at lower latitudes because of, for example, narrower environmental distributions of populations[103,104] and greater stochastic changes in biotic communities.[88,102] The higher levels of geographic genetic differentiation among populations at lower than higher latitudes[105] are consistent with such a view.

Acknowledgments

Conflicts of interest

The authors declare no conflicts of interest.

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