

Phenology and Interspecific Ecological Interactions of Andean Biota in the Face of Climate Change

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Complex links between phenology, the ecological interactions between species, and climate will determine the fate of species and ecosystems under climate change, but they are still poorly understood for the tropical Andes. In this chapter we use generalizations from temperate regions along with studies from the Andes and other tropical areas to discuss effects of climate on the phenology and interspecific interactions of tropical organisms, and to explore potential effects of climate change.

Phenology describes the timing of transitions between stages in organisms' life cycles. Phenology can be directly affected by climate (arrow 1 in Figure 4.1), for instance when organisms can only reproduce under certain climatic conditions because of physiological constraints (Morin 1999). Phenology plays a crucial role in the carbon balance of terrestrial ecosystems (Cleland et al. 2007) and vegetation feedback into the atmosphere (Schwartz 2003b).

Ecological interactions between species may affect the "fitness" of organisms, measured as their genetic contribution to the next generation, or they can affect population size (Futuyma 1998). Such ecological interactions include predation, competition, herbivory, parasitism, detritivore-detritus interactions, and mutualism (Ricklefs and Miller 2000). These interspecific interactions can be affected by climate in multiple ways (arrow 2 in Figure 4.1) when climate affects behavior (e.g., predator search efficiency) or physiology (e.g., herbivore metabolic rate). Interactions such as mutualisms between plants and mycorrhizal fungi play important roles in ecosystem carbon cycling (Pendall et al. 2004). Indeed, the functioning of virtually all ecosystems, and thus their impact on the atmosphere, depends on coevolved interspecific interactions (Thompson 2009).

Phenology can affect interspecific interactions (arrow 3, Figure 4.1) by altering the time overlap between interacting phenophases (Morin 1999), such as that between flowering or fruit set and pollinators or seed dispersers. Interspecific interactions can in turn affect phenology (arrow 4, Figure 4.1) because predators, competitors, herbivores, parasites, and mutualists exert pressures on the life cycle stages of other species (Morin 1999). Both

phenology and interspecific interactions can to some extent also affect local climate (arrows 5 and 6 in Figure 4.1), for instance through transpiration which depends on leaf activity. Water dynamics in the Amazon basin are largely influenced by forest cover (Chagnon and Bras 2005), and thus forest phenology.

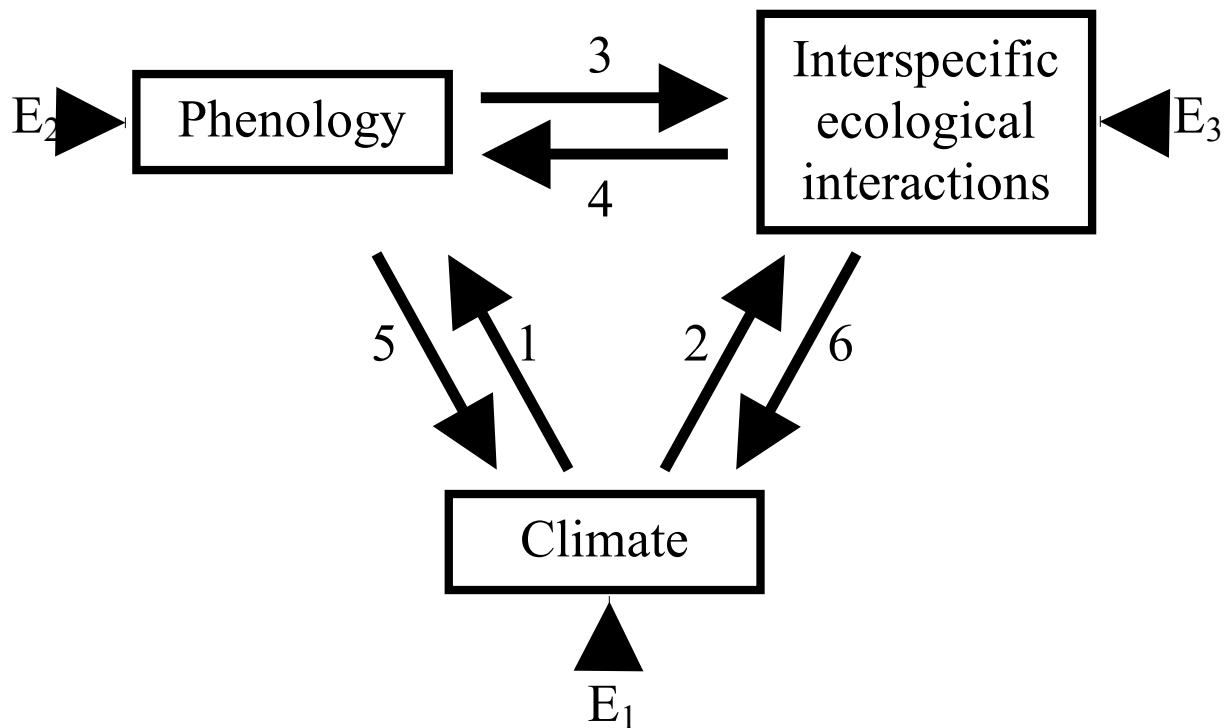


Figure 4.1. Graphical representation of a general structural equation model (Grace 2006) for the relationships among phenology, interspecific ecological interactions, and climate. Each box represents an observed variable related to phenology (e.g., flowering time), interspecific ecological interaction (e.g., frequency of visits to flowering plant by pollinators), and climate (e.g., monthly precipitation). Arrows between boxes represent causal relationships between the observed variables. E_1 , E_2 , and E_3 represent error terms subsuming all factors that affect the observed variables and are not explicitly considered.

Effects of Climate on the Phenology of Tropical Organisms

To examine how climate affects phenology we distinguish between "proximate" and "ultimate" causes (van Schaik et al. 1993). Proximate causes are the environmental stimuli as well as the genetic and physiological mechanisms that determine the function of a phenotype. Ultimate causes are the evolutionary forces that shape a phenotype, which is the physiology, morphology, and behavior of an individual organism. For example, the rapid flower closure in Andean plants of the genus *Gentianella* is proximately caused by climatic stimuli such as temperature and pressure changes that result in turgor loss and bending of plant organs (Claus 1926, Sibaoka 1991). The ultimate cause of this rapid flower closure may be evolution by natural selection as plants with rapid flower closure may better protect floral organs and pollen from damage by rain and other factors (He et al. 2006).

The ultimate causes of tropical plant phenology may be related directly to climate (arrow 1, Figure 4.1) in two ways. First, climate can limit plant production by lack of water

and sunlight (van Schaik et al. 1993). For instance, many tropical woody plants lose their leaves during the dry season (Sanchez-Azofeifa et al. 2003) and show peaks of foliage production and flowering at the onset of the rains (Reich and Borchert 1982, Morellato 2003). Water availability may also regulate leaf production in some understory plants of a lowland Neotropical forest (Aide and Angulo-Sandoval 1997). Second, climate can determine the abiotic conditions for dispersal or survival of particular phenophases (van Schaik et al. 1993). Plants pollinated and dispersed by wind tend to produce flowers and seeds during the windiest part of the year (Foster 1982, Charles-Dominique et al. 1981, Stevenson 2004). In areas with strongly seasonal water availability, the fruiting time of species may coincide with the onset of the rains (Foster 1982, Garwood 1983), presumably timing seed germination to the season with adequate moisture.

The ultimate causes of plant phenology may also be related indirectly to climate through its effects on interspecific interactions (arrows 2 and 4 in Figure 4.1). Climate can determine seasonality in the abundance of pollinators, seed dispersers, and other mutualists which, in turn, may support selection for a particular phenological schedule (van Schaik et al. 1993). Determining cause and effect is often difficult because the reverse direction of causality is possible: the abundance of animal mutualists may be determined by the availability of plant resources. For example, the Amazonian ant species *Allomerus octoarticulatus* breeds at the time of highest availability of nests provided by the hollow stem chambers (domatia) in the plant *Cordia nodosa*, which in turn seems to be determined by insolation (Frederickson 2006). Climate may also determine the seasonal abundance of natural enemies, selecting for plants that time their phenology to avoid herbivores (van Schaik et al. 1993). For instance, herbivores in seasonal forests may be less abundant during the dry season, and plants producing new leaves at that time may experience reduced herbivory (Aide 1988).

Proximate causes of tropical plant phenology sometimes also relate to climate. Trees with shallow roots occurring in forest with strongly seasonal rainfall patterns drop their leaves and arrest growth in response to water stress during the dry season, and flush leaves, flower and resume growth in response to the rainy season (Borchert 2004). However, some deciduous species drop their leaves before water stress occurs and start producing new leaves before the onset of rains, suggesting that water availability may not be the proximate cause of vegetative phenology, although it may well be its ultimate cause (van Schaik et al. 1993). Severe dry seasons during El Niño years may serve as proximate cues for tropical plants to increase reproductive efforts in anticipation of abiotic environments conducive to seedling establishment (the ultimate cause) during a milder dry season the following year (Wright et al. 1999). Supra-annual climatic oscillations such as El Niño may provide cues for supra-annual phenological patterns, synchronized across single or multiple species, which may serve to satiate predators or attract pollinators (Wright et al. 1999, Kelly and Sork 2002, Sakai et al. 2006, Brearley et al. 2007). In those cases the proximate cause is climatic, but the ultimate cause is related to biotic effects. Bamboo species of the genus *Chusquea* are conspicuous elements of several habitats across the tropical Andes and have supra-annual flowering phenology (Judziewicz et al. 1999), which may be triggered by cues related to El Niño (Jaksic and Lima 2003). High inter-annual variance in the phenology of tree species may be more common in the Neotropics than previously thought and could be associated to climatic cues (Norden et al. 2007).

Other factors than rainfall also provide ultimate and proximate causes of tropical plant phenology (Figure 4.1; Ratchcke and Lacey 1985, Borchert 2004). Drought tolerant plants with deep root systems, small leaf area, or low xylem resistance to water flow, for instance, may not be limited by seasonal water availability. For such species, and in areas with little seasonality in water availability, insolation may be a more important ultimate cause of

phenology (Wright and van Schaik 1994). This is because young leaves are most efficient at photosynthesis and plants may maximize fitness by producing them during times of highest insolation. Flowers may also be produced at this time because it is more efficient to transfer the products of photosynthesis directly to growing organs than to store and mobilize them later. Consistent with this idea, leaf flush and flowering in forests with weak rainfall seasonality reach a maximum during months with little cloud cover and highest insolation (Wright and van Schaik 1994, Huete et al. 2006). Similarly, leaf flush and flowering of drought tolerant species in strongly seasonal forests is timed for maximal insolation (Wright and van Schaik 1994). Seasonal variation in solar radiation is thought to be an important proximate cause for synchronized flowering in tropical plants that allows cross pollination (Rivera et al. 2002, Borchert et al. 2005, Yeang 2007, Rivera and Cozza 2008). Although variation in solar radiation is small in the tropics relative to temperate areas, plants are able to use it as a cue. The mechanism of this sensitivity to photoperiod is not well-understood (Renner 2007).

Inter-specific staggering of phenologies may evolve as a response to non-climatic factors such as competition for pollinators and dispersers, or to avoid interspecific pollination and hybridization (van Schaik et al. 1993, Morin 1999). Competition for pollinators was indicated in a study showing that fertilization of plant ovules in diverse tropical communities is limited by pollen availability (Vamosi et al. 2006). Thus it may play a role in the flowering times of *Bombacaceae* species (Lobo et al. 2003) or the temporal patterns of fruit production in *Piper* species (Thies and Kalko 2004). Phenological studies of trees in the tropical Andes (Bendix et al. 2006, Gunter et al. 2008) and elsewhere in the tropics (Stevenson 2004, Chapman et al. 2005) illustrate the wide range of phenological patterns exhibited by different species, and indicate that multiple proximate and ultimate causes are at play at any single site.

Strong seasonal variation in activities like reproduction and migration is well known for birds in temperate regions, where variations in climate are pronounced. By contrast, Neotropical birds generally exhibit much less seasonality in their phenology (review by Stutchbury and Morton 2001). Within a given community, Neotropical birds may breed at all times of the year, frugivores often in the dry, insectivores in the wet season. The breeding seasons of individual species are 2-3 times longer than those of temperate zones. However, one cannot conclude that aseasonal breeding patterns are typical for the tropics based on a few single-species studies from lowland rain forest localities (see Stutchbury and Morton 2001). Detailed studies of the spotted antbird (*Hylophylax n. naevioides*) in a lowland forest of Panama, for instance, have documented strongly seasonal breeding, starting at the beginning of the rainy season (Wikelski et al. 2000). Gonad enlargement in this species responds to small variations in photoperiod, allowing spotted antbirds to anticipate the rainy season (Hau et al. 1998). Further experimental work showed that these birds fine-tune the timing of gonad growth and reproductive behavior using additional proximate cues, including the opportunity to "handle" or see live insect prey (Hau et al. 2000). These studies documented proximate causes of breeding phenology, but the ultimate causes remain largely unknown. Such synchronous breeding at the onset of the rainy season may be explained by selective pressures associated with food availability, reduced predation risk, and the need to avoid molting and breeding simultaneously (Wikelski et al. 2000). In contrast, breeding activities of birds that live in unpredictable habitats, such as small ground finches (*Geospiza fuliginosa*) in the Galapagos archipelago, may not be triggered by photoperiod, but rather by cues that are more directly related to reproductive success, such as rainfall or barometric pressure (Hau et al. 2004). These detailed studies on selected species illustrate what might be common proximate causes of bird phenology, and hint at possible ultimate causes as well.

Very little has been published on the phenology of bird reproduction in the tropical Andes. A study in the Andes of Colombia (Miller 1963), where rainfall is bimodal with peaks

of precipitation in March-May and October-November, revealed a reproductive peak at the community level during the first rainy season of the year, but some species bred throughout the year independent of rainfall, and a few species bred during the dry season. Some thrushes (Turdidae) breed during the first and molt during the second rainy season of the year (Beltrán and Kattan 2001). A recent study (S.K. Herzog, unpubl.) in inter-Andean dry valleys in Bolivia showed that avian reproduction is highly seasonal and largely restricted to the austral spring and summer, showing similar degrees of synchronization as temperate bird communities. The overriding factors for the timing of breeding are precipitation and insect biomass, which itself is highly correlated with precipitation. This makes sense intuitively, because inter-Andean dry forests have a more seasonal climate than lowland rainforests. Therefore, avian phenology in the tropical Andes can be expected to become increasingly seasonal with increasing seasonality in climatic parameters, especially in drier habitats where greater seasonal variation in precipitation can be expected to have a pronounced impact.

Even less is known about migration in Andean birds. Species in the Andes can generally be divided into three categories of migration systems: (1) Long-distance Nearctic-Neotropical migrants that spend the northern-hemisphere winter in the tropics; (2) Austral migrants that breed in the southern temperate zone and spend the Austral winter in the tropical Andes; and (3) intratropical migrants that are either year-round residents migrating altitudinally or latitudinally within the tropical Andes, or breeding Austral summer residents that migrate to lowland areas at the end of the Austral summer. Several species also perform more nomadic long-range movements to track patchy food resources such as mass-seeding bamboo. Intra-Andean migrants, especially altitudinal migrants, are perhaps the most relevant group in the present context. The extent and magnitude of altitudinal migration in Andean birds is largely unknown, and so are the environmental cues that determine migration timing. As with reproductive phenology, climatic factors such as precipitation may play an important role. In some cases, avoidance of temporal overlap and resulting competition for food resources between Nearctic-Neotropical and intra-Andean migrants (e.g., *Catharus ustulatus* and *Turdus nigricaps*, respectively) may be important.

Climate, particularly precipitation, is related to the phenology in many other vertebrates. The phenology of bats in montane forests between 1300-1750 m of the eastern Andean slopes in Bolivia (Montaño 2007) showed various seasonal reproductive peaks per year. This was related to resource availability which, in turn, was linked to precipitation, so that most females are pregnant at the time of maximum rainfall. During the dry season Andean amphibians are exceedingly hard to find, but with the first rains they burst out into an impressive chorus that ranks among the most spectacular biological phenomena in the Andes. Reproductive activity of *Agalychnis* tree frogs and microhylids are known to be extremely seasonal related to rainfall patterns (Gottsberger and Gruber 2004; Stuart et al. 2008). Ground-dwelling amphibians and reptiles may respond to seasonal variations in soil humidity. Reproductive cycles of tropical freshwater fishes, particularly in mountain streams, remain poorly understood, but are likely to be tightly linked to stream flow and rainfall changes. Whereas lowland fish species inhabiting floodplain rivers are thought to primarily spawn during the wet season (reviewed by Munro et al. 1990), several fish species inhabiting mountain streams have been shown to spawn during dry periods (Torres-Mejia and Ramírez-Pinilla 2008 and references therein). Climate-induced variations in river flow, in terms of timing, duration, and magnitude of high and low flow events, could provide cues to migratory species that live, feed, or spawn in Andean piedmont rivers (e.g., *Prochilodus magdalenae*, *P. reticulatus*, *P. nigricans*, *Salminus affinis*).

The abundance and diversity of several Neotropical insect groups show marked seasonal variation, often low during the dry season and increasing at the onset of the rainy season (Wolda 1978, 1983, 1992; Smythe 1982; Janzen 1984; Wolda and Wong 1988; Brown

1991; DeVries et al. 1997). For instance, ant breeding flights peak at the onset of the rainy season in a lowland forest in Panama (Kaspari et al. 2001). The beginning of the rainy season may be the proximate cause of this pattern if it serves as a cue to synchronize breeding within species, and may also relate to ultimate causes because rainfall is thought to provide higher food availability and more suitable microclimates for breeding and colony foundation (Kaspari et al. 2001). Climate events such as rainfall also trigger the synchronized and extremely short-lived swarming events of termites in Atlantic rainforest of Brazil (Medeiros et al. 1999). Likewise, insect biomass and abundance closely correlate with precipitation in an inter-Andean dry forest of Bolivia (A.C. Hamel-Leigue and S.K. Herzog, unpubl.). Dung beetles (Scarabaeidae: Scarabaeinae) also show significant seasonal variations in species richness at the same site (A.C. Hamel-Leigue, D.J. Mann and S.K. Herzog, unpubl.). This indicates that reproductive cycles of many insects may be closely tied to climatic variables.

However, not all insect species respond to the same environmental cues or share similar ultimate causes of phenology. Some Panamanian ants perform breeding flights throughout the year (Kaspari et al. 2001). While most Atlantic rainforest termites swarm during the rainy season, dry-wood termites (Kalotermitidae) swarm in the dry season (Medeiros et al. 1999). Some species of dung beetles in the Bolivian Andes show patterns that contrast with the overall trend of minimum abundance during the height of the dry season. Compared to the Bolivian seasonal deciduous forest, dung beetle abundance and species richness varies little over the year in more tropical, evergreen forests in Peru (T. Larsen, pers. comm.). Thus, analogous to the timing of breeding in tropical Andean birds, insects can be expected to become increasingly seasonal with increasing seasonality in one or more climatic parameters.

Temporal variation in the life cycle stages of Neotropical fungi relates to variation in precipitation. Mycelial activity and abundance of fruiting bodies of leaf litter fungi in tropical forests is related to seasonal variation in water availability (Hedger 1985). High temporal turnover in species suggests that different fungi species in lowland tropical forests show strong seasonality related to rainfall (Lodge and Cantrell 1995). Variation in mycorrhiza spore abundance is also correlated to rainfall seasonality (Janos et al. 1995, Guadarrama and Álvarez-Sánchez 1999). At shorter time scales, the cumulative rain during three days was positively related to the diversity of fungal fruiting bodies in leaf litter of a central Amazonian forest (Braga-Neto et al. 2008). Deposition of endophyte hyphal fragments and spores on lowland tropical understory leaves is high just after rainfall events and decreases markedly as hours pass (Arnold 2008). In general, the temporal and spatial distribution of tropical forest fungi suggests that different species are adapted to different climate or weather conditions (Lodge and Cantrell 1995), but rigorous studies aimed to understand proximate and ultimate causes of the phenology are scarce.

Cycles of macroinvertebrate abundance in forest leaf-litter vary with precipitation and moisture content of the litter (Kattan et al. 2006, Levings and Windsor 1996). Abundance of bacteria in tropical forest leaf-litter is affected by water availability (Cornejo et al. 1994, Lodge et al. 1994, Yavitt et al. 2004). The life cycles of many parasites are affected by climate. Temperature affects the emergence of free swimming stages of trematode parasites from their snail hosts (Poulin 2006), and determines development and survival of Apicomplexan protistan organisms such as *Cryptosporidium parvum* (Fayer et al. 1998), a parasite of mammalian intestines causing cryptosporidiosis. Abundance of the causative agent of human malaria, *Plasmodium falciparum*, is similarly climate dependent (Paaajmans et al. 2009). A complete review of these patterns across taxonomic groups is outside the scope of this chapter, but it is clear that the phenology of Neotropical organisms is linked to climate, and to precipitation in particular.

Effect of Climate on Interspecific Interactions of (Neo)tropical Organisms

Climate may determine the nature of interspecific interactions in multiple ways and at a variety of temporal and spatial scales, as seen in the examples in previous paragraphs. Here we examine just a few ways that seem particularly important in the context of future climate change in the tropical Andes. Spatial variation in climate can affect the outcome of ecological interactions. For instance, climate often determines the geographic range of species (Gaston 2003, Sexton et al. 2009; see also Larsen et al. Chapter 3, this volume) and thus where species overlap geographically and interact. Altitudinal species turnover in the tropical Andes has been argued to result from interactions in which some species are excluded from particular elevations by competitively superior species, while the elevational range of the latter species is limited by climatic factors (Terborgh and Weske 1975, Remsen and Cardiff 1990, Remsen and Graves 1995). Recent empirical support for this hypothesis derives from studies of Andean birds and mammals (Anderson et al. 2002, Cadena and Loiselle 2007, Herzog et al. 2009). Likewise, inter-annual variation in precipitation may determine the geographic range of specialized parasitoid wasps, creating a spatial gradient of parasitism in caterpillars (Stireman et al. 2005). Even within the geographic range of a species climate can alter ecological interactions through its effects on phenotypes. Flight performance of Andean hummingbirds is influenced by climatic factors that change with elevation, with consequences for territorial behavior and competitive interactions (Altshuler 2006).

Temporal variation in climate can also have major effects on ecological interactions. Temporal variation in incidence of diseases such as malaria, influenza, and West Nile virus has been correlated to climate, although the causal structure underlying these correlations can be complex (Lafferty 2009). Prolonged drought can reduce habitat size in tropical forest streams, potentially increasing the strength of interspecific interactions due to crowding (Covich et al. 2003). El Niño southern oscillation has affected plant phenology in a Neotropical forest (see above) and thereby the population dynamics of fruit and seed eating animals (Wright et al. 1999). Pronounced drought during an El Niño year in a Borneo lowland rainforest lead to failure in the production of flowers by fig trees (*Ficus* spp.), resulting in local extinction of their Agaoninae wasp pollinators (Harrison 2000). Species of these wasps require fig trees to reproduce and vice versa, and fruits of fig trees are important resources for many vertebrates (Herre et al. 2008). Thus, local extinction of fig-pollinating wasps could potentially trigger changes in the composition of vertebrate frugivore communities (Harrison 2000).

The effect of climate on interspecific interactions played over long evolutionary time may have had a major impact on the nature of tropical ecosystems, including those in the tropical Andes. For instance, the contrast between tropical dry and rain forest in rainfall seasonality results in major differences in temporal patterns of foliage availability for herbivores and may have resulted in stronger selection pressures for increased plant defense in rain forest plants (Dirzo and Boege 2008). Moreover, little variation in temperature at seasonal (Vazquez and Stevens 2004) and geological (Imbrie et al. 1993, Weaver et al. 1998) time scales may have allowed interspecific ecological interactions to be more important selective pressures in the tropics than in temperate regions. Evidence supporting this idea derives from a variety of sources (Schemske et al. 2009). For instance, the effects of herbivores on plants (Coley and Aide 1991, Dyer and Coley 2002), effects of predators and parasitoids on herbivores (Dyer and Coley 2002), predation pressure from ants on other insects (Novotny et al. 2006), and bird nest predation rates (Schemske et al. 2009) appear to be higher in the tropics than in temperate latitudes. The frequency of animal pollinated (Regal 1982) and animal dispersed (Moles et al. 2007) plants is much higher in the tropics than in temperate regions. About 90% of tropical plants depend on animals for pollination or seed

dispersal (Jordano 2000; see Krömer et al. 2006 for a tropical Andean example). Interactions in which symbiotic ants live in specialized plant structures are far more common in the tropics (Davidson and McKey 1993). Endophytic fungi can provide plants with herbivore defenses (Herre et al. 2007) and their incidence is higher in the tropics (Arnold and Lutzoni 2007). These patterns suggest that interspecific ecological interactions are particularly important for the structure and function of tropical ecosystems, and that disruption of such interactions due to climate change may have far-ranging consequences.

Potential Effects of Future Climate Change on Phenology and Interspecific Interactions of Andean Organisms

Scenarios of Future Change in Climatic Parameters Correlated to Phenology of Andean (or Neotropical) Organisms

The studies mentioned in previous sections suggest that proximate and ultimate causes of the phenology of many Andean organisms relate to the spatial and temporal distribution of precipitation. This is consistent with studies showing that precipitation drives general phenology in several Neotropical biomes (Reich 1995, Asner et al. 2000, Morellato 2003, Sanchez–Azofeifa et al. 2003). A prominent exception is the effect of temporal variation in solar insolation on plant phenology (see above). But even in this case, in many (but not all) sites temporal variation in insolation is associated with cloud cover and thus related to temporal variation in precipitation (Wright and van Schaik 1994, da Rocha 2004). Thus we focus on temporal and spatial patterns of precipitation as key abiotic drivers of phenology in the tropical Andes, while acknowledging that other abiotic factors may also be important. Ideally, we would like to know which particular parameters of the distribution of precipitation (e.g., amplitude of rainfall peaks, length of the dry and rainy seasons) determine phenological patterns of Andean organisms overall, and the future trends of such parameters. Some of the climatic data available allow the estimation of many detailed descriptors of rainfall seasonality (Figure 4.2) that would allow to test different possibilities, but phenological data for the tropical Andes are scant (Morellato 2003, see above). To overcome this limitation, below we point out three kinds of future changes in climate that might have important impacts on the phenology of tropical Andean organisms.

First, total annual precipitation may change, with increasing trends in some regions and decreasing in others such as inter-Andean valleys (Marengo et al. Chapter 7, this volume). Effects on phenology are likely to be non-linear and depend on relative rather than absolute change. For instance, a 200 mm decrease from currently 1,000 mm of annual precipitation (Figure 4.3) may result in a shift from moist forest to dry forest life zones (Holdridge 1947) while a change of the same magnitude in a place receiving 3,000 mm would maintain a wet forest. A similar case could be made for areas that currently receive around 100 mm of monthly precipitation during the driest month (Figure 4.4). Second, although there are no studies in the tropical Andes, in the south of the continent the amplitude of the annual precipitation cycle may be increasing (IPCC 2007). This may cause increased seasonality in phenology (see above). Third, warming trends will affect elevation profiles of relative humidity, shifting the location of orographic cloud banks that supply significant amounts of water to Neotropical mountain forest (Pounds et al. 2005; Ruiz et al. Chapter 12, this volume). In some areas these shifts may increase the number of dry days per year, lengthening the dry season or interrupting the wet season (Pounds et al. 2005). This would

likely create seasonally stressful environments and a more seasonal phenology (Ruiz et al. Chapter 12, this volume).

Cusco - Perayoc (3,365 m) daily precipitation rate 1963-2004

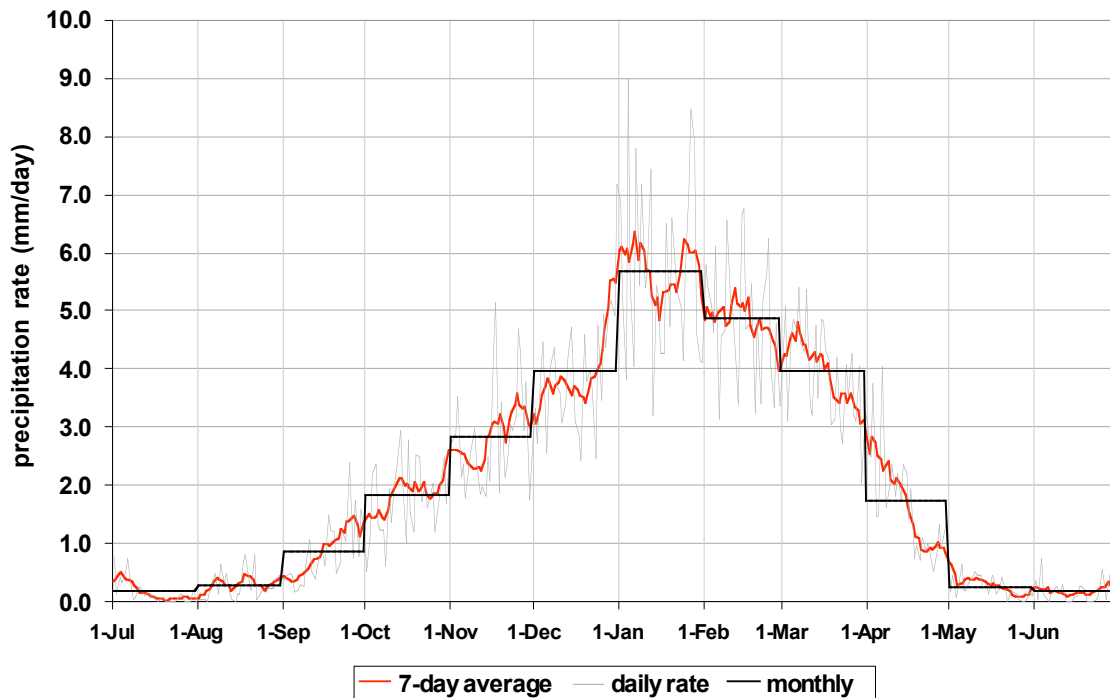


Figure 4.2. The daily mean precipitation rate over the July-June hydrological year at Cusco over the 42-year period 1963-2004 shown as daily values, 7-day running averages and monthly means. The abrupt intensification of wet season rainfall is a common characteristic for many locales in the central Andean region, yet is unrecognized in the scientific literature where monthly statistics are mostly presented to characterize rainfall, rather than the daily resolution required to capture such high-frequency behavior. The ecological significance of such behavior is unknown, though it may act to trigger phenological responses in and among species. (Data analysis by A. Seimon).

Beyond the three changes highlighted above, other future climatic changes are likely (Anderson et al. Chapter 1 and Marengo et al. Chapter 7, this volume), primarily associated with the behavior of the Pacific High, the Bolivian High, and the Intertropical Convergence Zone (see Martínez et al. Chapter 6, this volume). Although some trends can be suggested based on extrapolation of already observed changes in temperature and precipitation, it would be useful to develop studies specifically on variables likely to affect the phenology of tropical Andean organisms, including descriptors for the seasonality and inter-annual variation of precipitation.

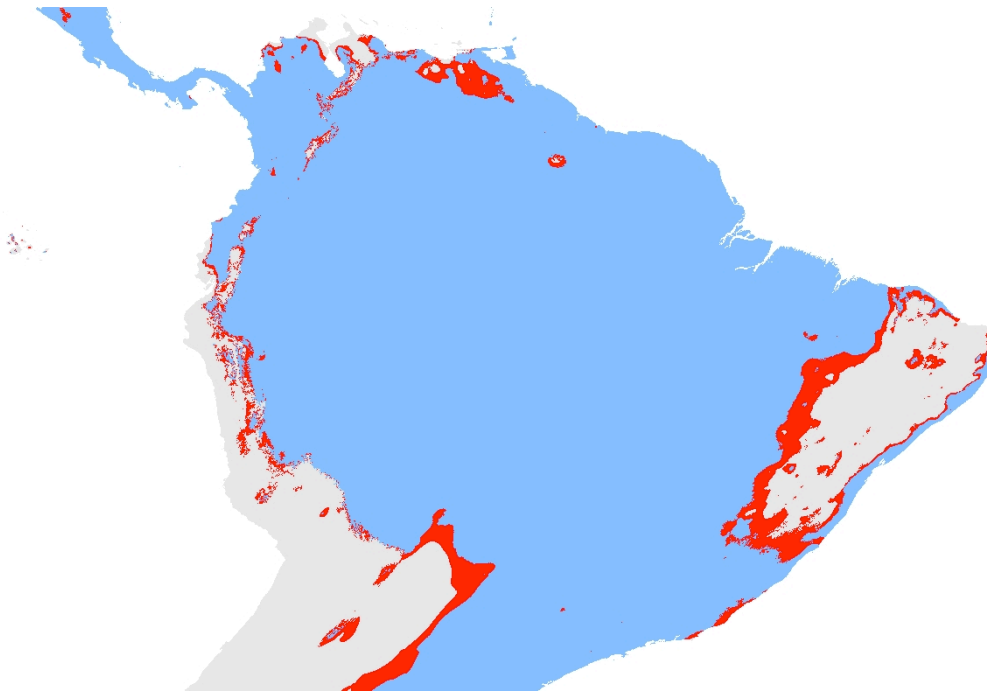


Figure 4.3. Geographic distribution of areas with annual precipitation <900 mm (gray), 900 mm – 1,000 mm (red), and >1,000 mm (blue). From Worldclim (<http://www.worldclim.org/methods.htm>).



Figure 4.4. Geographic distribution of areas with precipitation of the driest month <90 mm (gray), 90 mm – 100 mm (red), and >100 mm (blue). From Worldclim (<http://www.worldclim.org/methods.htm>).

Potential Impacts of Climate Change on Phenology of Andean Organisms

We are unaware of studies on the effect of ongoing climate change on the phenology of tropical Andean organisms, so we use examples from elsewhere to explore possible scenarios. Responses to climate change depend on how climate relates to proximate and ultimate causes of phenological patterns. When climate is closely related to both the proximate and ultimate causes of phenological patterns, climate change may be expected to have immediate effects on phenology. Likely examples of such instances are seasonally deciduous trees (Borchert 2004, see above) or birds that time their breeding using climatic cues (Hau et al. 2004, see above). In these cases phenological adaptation may ameliorate negative impacts of climate change on fitness (Parmesan 2006).

When climate is closely related to ultimate but not proximate causes of phenological patterns, climate change may decrease fitness due to a mismatch between the cues triggering phenological events and the factors determining survival and reproduction. For instance, plants that drop leaves anticipating the water stress characteristic of the dry season may be using non-climatic cues (van Schaik et al. 1993, see above). Likewise, spotted antbirds use changes in photoperiod to gradually enlarge gonads in preparation for breeding during the rainy season (Hau et al. 2000, see above), when high availability of invertebrate prey is conducive for successful reproduction (Wikelski et al. 2000). If climate change alters the correlation between cues such as photoperiod and the factors that determine fitness such as water or prey availability, a decrease in fitness may result. Temperate plants and birds provide examples of this. In eastern North America, plants' ability to shift flowering time with climate change affects abundance, with species that have not shifted their phenology decreasing in abundance (Willis et al. 2008). Migratory bird species that have not shifted their arrival time at their breeding grounds in response to climate change appear to be declining in abundance too (Both et al. 2006, Miller-Rushing et al. 2008, Møller et al. 2008). Decreasing fitness, however, creates selective pressures that may result in evolution of responses to environmental cues, as documented for organisms as diverse as insects, birds, and mammals (Bradshaw and Holzapfel 2006). Such evolutionary responses may or may not be enough to halt population decline.

When climate is closely related to proximate but not ultimate causes of phenological patterns, climate change will likely result in phenological change, but the impact on fitness may be particularly difficult to predict. For instance, climatic cues may synchronize flowering or fruiting across one or several species. Such synchrony may increase fitness by increasing pollinator attraction or predator satiation (van Schaik et al. 1993, see above). As long as the climatic cue still occurs, organisms may still be able to synchronize their phenology and climate change may have little impact on their fitness. On the other hand, if different climatic cues are used by different species to stagger their phenologies and avoid interspecific competition for pollinators and seed dispersers (see above), climate change may result in more overlapping phenologies and decreased fitness. Species may then evolve responses to the changes in cues and thus adjust their life cycles according to the fitness consequences. We emphasize that this section is only an exploration of possible scenarios, and that predicting consequences of climate change for phenology and fitness is notoriously difficult due to the complexity of the relationships between climate, phenological patterns, and ecological interactions (Figure 4.1).

Potential Effects of Climate Change on Interspecific Interactions of Andean Organisms

Responses to climate change are species-specific because species differ in their ecological tolerances, life-history strategies, and dispersal and evolutionary abilities (Parmesan 2006). If species differ in their responses to a changing climate, ecological interactions may be affected in several ways. Here we discuss three potential outcomes: alteration of the timing of the interaction (temporal mismatch), shifts in geographic ranges (spatial mismatch), and changes in phenotypes or abundances of interacting species.

First, interacting species may differ in their phenological responses to new environmental conditions, altering the timing of the interactions. We know of no examples from the tropical Andes, but there are many examples elsewhere. Effects of climate on plant phenology (Cleland et al. 2007) can temporally decouple mutualistic interactions with animal pollinators (Memmott et al. 2007), as mentioned above for fig trees and wasps (Harrison 2000). Changes in phenology can also alter mutualistic relationships between plants and seed dispersers (Jordano 2000, Ness and Bresmer 2005), and antagonistic interactions between plants and insect herbivores (Visser and Holleman 2001, Visser and Both 2005, Musolin 2007, van Asch and Visser 2007). The latter can further propagate through trophic levels resulting in bird reproduction that is no longer synchronous with the abundance of their herbivore insect prey (Visser et al. 2004) as well as reproduction of top predators that does not match the abundance of their bird prey (Both et al. 2009). Effects of climate on phenology can alter the timing of interspecific interactions through the so called “priority effects” in which the order of species arrival to a local community inhibits or facilitates the arrival of other species (Morin 1999). For example, winter warming in Britain resulted in earlier breeding in newts (*Triturus* spp.) but no similar response occurred in frogs (*Rana temporaria*), so that early developmental stages of the latter species are exposed to higher predation pressure by newts (Beebee 1995). Climate can play a role in priority effects that seem common in the infection of tree roots by mycorrhizal fungi, with implications for the performance of both symbionts (Kennedy et al. 2009).

Second, species may respond to climate change by shifting their geographic ranges (Jackson and Overpeck 2000, Parmesan 2006, Moritz et al. 2008), thereby affecting interactions. For instance, ongoing climate change is likely to contract the geographic range of leaf spurge (*Euphorbia esula*), an invasive plant now dominating ecosystems west of the Mississippi River, thus potentially releasing many species from a negative interspecific interaction and creating opportunities for the recovery of ecosystems (Bradley et al. 2009). Climate change is likely to expand the range of other introduced species resulting in opposite effects, as illustrated by experimental work on native (*Eriopis connexa*) and exotic (*Hippodamia variegata*) ladybird beetles in the Andes of central Chile (Molina-Montenegro et al. 2009). Climate change is also likely to result in spatial mismatch between a monophagous butterfly species (*Boloria titania*) and its larval plant host (*Polygonum bistorta*) in some European regions (Schweiger et al. 2008). Just as shifts in geographic ranges may interrupt interactions, they may result in new interactions among species. Avian malaria in Hawaii restricts native bird species to higher elevations (van Riper et al. 2003) where temperature halts appropriate development of the malaria pathogen inside its mosquito vector (*Culex quinquesfasciatus*, LaPointe et al. 2005). Yet, the incidence of avian malaria at higher elevations has increased over the last decade in association with increasing temperatures (Freed et al. 2005). High elevation Andean avifaunas may be similarly at risk from expansion of the geographic ranges of pathogens due to climate change (LaPointe et al. 2005). Vampire bats, *Desmodus rotundus*, are recognized reservoirs for the rabies virus, and their distribution is generally restricted to areas of warmer climates (McNab 1973, Greenhall

et al. 1983). They seem to have moved upslope in Costa Rica during the last decades (LaVal 2004), extending the altitudinal range of their interaction with hosts and the rabies virus.

Third, species may remain in place and synchronized, but climate change can alter the phenotype (physiology, behavior, and morphology) or abundance of interacting species, thereby changing the outcome of the interaction. Temperature and humidity affect nectar concentration and secretion rate, which in turn affect pollinator behavior and, potentially, plant and pollinator fitness (Petanidou 2007). Climatic variation can directly affect the behavior of top predators, with repercussions through trophic cascades. Changes in winter climate related to the North Atlantic Oscillation caused Isle Royal wolves (*Canis lupus*) to hunt in larger packs, resulting in higher predation of moose (*Alces alces*) and consequent decreased herbivory and increased growth of balsam fir (*Abies balsamea*, Post et al. 1999). Climate variation directly affects the population dynamics at each trophic level in Isle Royal (wolves, moose, and fir), most strongly at the top and bottom trophic levels, and has the potential to threaten the persistence of the ecological community (Post and Forchhammer 2001). The negative impact of decreased water availability on the abundance of herbivore parasitoids and subsequent increase in herbivory rates may be one of the major effects of future climate change on tropical forests (Coley 1998). The effect of climate on species abundance can affect species interactions as diverse as mutualisms between plants and their pollinators or plants and ants, as well as antagonistic interactions between fish and metazoan parasites or mammals and fleas (Vásquez et al. 2007), because abundance determines the frequency of encounters among individuals of the different species which determines the strength of interactions.

Although there seems to be little documentation of the impacts of climate change on ecological interactions in the tropical Andes, there are reasons to believe that these impacts may be at least as important as in temperate regions. First, experimental studies of Neotropical organisms show the existence of strong effects of biotic interactions, such as the effect of herbivory on species distribution across habitats (Fine et al. 2004) and strong tritrophic interactions (Boege and Marquis 2006). Likewise, other studies of Neotropical organisms demonstrate that disrupting interspecific ecological interactions results in major impacts on the abundance and distribution of organisms. Studies of forest fragments that have lost predators of vertebrates document decreased availability of pollinators and seed dispersers, increased density of invertebrate predators, rodents, and herbivores, higher tree sapling mortality, and lower sapling recruitment (Terborgh et al. 2001, Terborgh and Feeley 2008). Local extinction of large vertebrates affects tree regeneration in other Neotropical forests as well (Dirzo and Miranda 1990, Terborgh et al. 2008). Indeed, ecological interactions may be particularly important in the structure and function of tropical ecosystems over both ecological and evolutionary time scales (Schemske et al. 2009, see above).

Second, specialization in ecological interactions may be more common in Neotropical than temperate ecosystems, as exemplified by the number of host plant species used by herbivore insects (Dyer et al. 2007, but see Novotny et al. 2006, Ollerton and Cranmer 2002). Specialization, however, is a major constraint that hinders response to temporal environmental change and thus contributes to extinction risk (Colles et al. 2009). In contrast to specialized ecological interactions, interactions may occur in diffuse networks involving multiple species. For example, the fruits of trees and shrubs are consumed by many different species of birds which disperse their seeds, and conversely, each bird species will feed on many different fruits (Figure 4.5). While bird species may differ in their role in seed dispersion due to differences in both the consumption and subsequent deposition of viable seeds (Schupp 1993), the multiple interacting species provide a redundancy of ecological roles that make the system robust to the extinction of individual seed dispersers (Loiselle and Blake 2002).

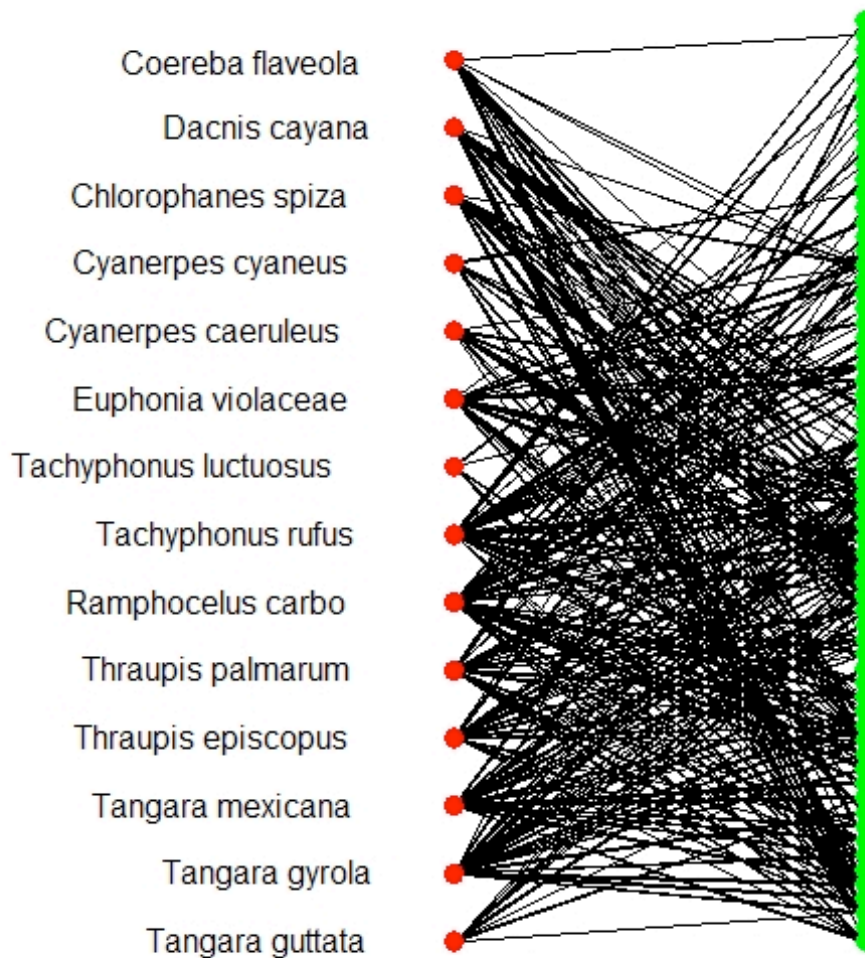


Figure 4.5. Network describing interactions between 65 plant species (green points) and 14 bird species (red points) that fed on their fruits in Trinidad from August 1960 through September 1961 (Snow and Snow 1971). Data available at the Interaction Web Database (<http://www.nceas.ucsb.edu/interactionweb/index.html>), hosted by the National Center for Ecological Analysis and Synthesis.

Conclusions

Further work to understand impacts of climate change on phenology should examine alternative hypotheses about how abiotic factors (e.g., precipitation and insolation) and ecological interactions determine phenological patterns. Examining such hypotheses for the tropical Andes may be hampered by the paucity of phenological data for the region (Morellato 2003), although climate data available for some areas may allow estimation of relevant parameters in some detail (Figure 4.2). Future phenological studies can draw from a wide range of tools to challenge the predictions of different hypotheses, including “phenological networks” aiming to gather long-term observations of phenophases of wild species across regions (see chapters in part 2 of Schwartz 2003a), remote sensing, airborne pollen data, manipulative experiments, and spatial models to predict phenology (Cleland et al. 2007). The distinction between ultimate and proximate causes, as emphasized in this chapter, is crucial to the understanding of phenological patterns (van Schaik et al. 1993) and the prediction of the impacts of climate change (Bradshaw and Holzapfel 2006). Studies

regarding not only the relationship between phenology, climate, and other possible causal factors, but also regarding spatial and temporal variation in fitness will be helpful. Where ultimate and proximate causes of phenology are reasonably well understood, it would be useful to examine how climatic parameters related to both kinds of causes are likely to change. Analysis of observed tendencies and future scenarios, and predictive models of phenology and fitness under climate change are needed. Finally, the study of ecological interaction networks (Bascompte 2009) seems particularly useful because it focuses on properties describing the overall structure of networks of interacting species (e.g., Figure 4.5), such as the distribution of the number of interactions per species and the degree to which the network is nested (Figure 4.6). These characteristics of the overall structure of networks can be used to estimate the importance of different species for the persistence of ecological communities (Allesina and Pascual 2009), and to forecast the impact of multiple drivers of global change on biodiversity (Rezende et al. 2007, Tylianakis et al. 2008).

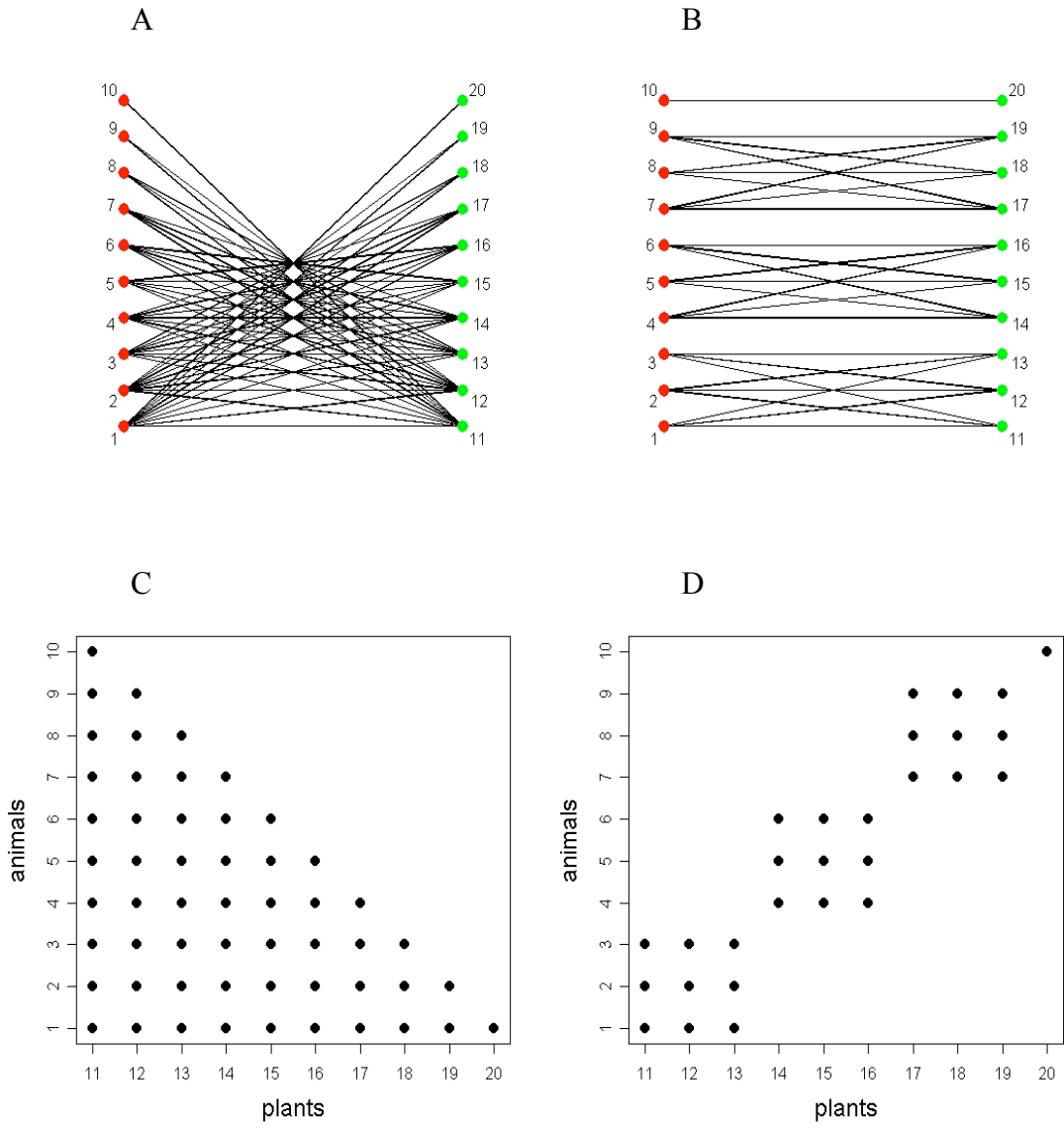


Figure 4.6. Illustration of interaction networks between plant (green dots) and animal (red dots) species with nested (A) and compartmentalized (B) structures. These networks are shown in plot form in C and D, respectively. This illustration is not based on real data. The robustness of networks of interacting species to temporal environmental change may depend on whether they are nested (Tylianakis et al. 2008). In nested networks generalist species interact with each other and with specialized species, while specialized species interact mostly with generalist species (A, C). Nested networks are relatively robust to disturbance because they depend on generalist species that can limit the effects of random species loss. In contrast, compartmentalized networks are composed of groups of species that interact strongly among them and only weakly with others (B, D), and are more susceptible to random species extinction. Mutualistic networks describing plant-pollinator or plant-seed disperser interactions may generally be nested and characterized by weak and asymmetric links (Jordano et al. 2003, Vázquez and Aizen 2004, Bascompte et al. 2003, 2006), while antagonistic interactions may be more compartmentalized and characterized by stronger links (Lewinsohn et al. 2006). Yet, networks of more intimate (i.e., symbiotic) interactions such as those between ants and myrmecophytes can also be highly compartmentalized (Guimaraes et al. 2007) and thus potentially more vulnerable.

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