

## A theoretical framework for understanding the ecology and conservation of bamboo-specialist birds

Juan I. Areta · Kristina L. Cockle

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**Abstract** Worldwide, populations of a diverse array of bamboo-specialist birds must respond to the life cycles of typical woody bamboos, which include a long vegetative phase, a short period in sexual reproduction (seeding), and a short period dead. While some bamboo species flower continuously in time, but scattered in space, over different parts of their distribution, others exhibit a single, synchronized mass-seeding event, followed by death over hundreds of square kilometers. Thus, bamboo-specialist birds experience extreme variability in their habitat and food sources, and may pass from a period of overabundant habitat and food resources to a period of extreme resource scarcity. At a community level, bamboo species are out of phase with each other. Masting events of several bamboo species may coincide one cycle, but not the next. The resulting long-term dynamics of bamboo cycles at a

community scale will result in a temporal and geographic mosaic of resource availability over very long periods of time, where the initial conditions that any bird experienced may occur only sporadically over centuries and very large regions. We aim to propose a theoretical framework for understanding the population ecology of bamboo-specialist birds and discuss implications for their conservation. Three main diet and life-history strategies of bamboo-specialist birds can be identified based on their natural history. First, insectivorous bamboo specialists that inhabit woody bamboos may be relatively sedentary during the long vegetative growth phase, but they must experience population declines, switch to alternative habitat, or travel widely during bamboo die-off events. They benefit from long-term habitat stability but must face short-term reductions in habitat that do not affect all generations of birds. Second, bamboo seed specialists must rely on an ephemeral source of food available only after large intervals of time at most locations. Since bamboo cycles are typically much longer than the lives of individual birds, there is no chance for seed-specialist birds to learn when and where bamboo seeds will be available in the future. Thus, although bamboo seed availability is ecologically predictable (i.e., seeds are always available after the same length of time at a given place), seed availability is unpredictable to individual birds. During their lifetime, most individual bamboo seed-specialists must face a lack of their preferred food supply, at which time they must wander to survive. And third, mixed strategists usually feed on bamboo shoots, leaves, and insects, but consume bamboo seeds when available. Their life history combines elements of both previous categories: they can benefit from long-term habitat stability like insectivores, and take advantage of masting events like seed specialists. Niche width (degree of specialization) in conjunction with the long-term dynamics

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J. I. Areta (✉) · K. L. Cockle  
Materi & España, CICyTTP-CONICET, Diamante 3105,  
Entre Ríos, Argentina  
e-mail: esporofila@yahoo.com.ar

J. I. Areta  
Grupo FALCO, 53 n 620 e/7 y 8,  
La Plata 1900 Buenos Aires, Argentina

K. L. Cockle  
Proyecto Selva de Pino Paraná, Fundación de Historia Natural  
Félix de Azara, Departamento de Ciencias Naturales Y  
Antropología, Universidad Maimónides, Valentín Virasoro 732,  
Buenos Aires C1405BDB, Argentina

K. L. Cockle  
Centre for Applied Conservation Research, Faculty of Forestry,  
University of British Columbia, 2424 Main Mall, Vancouver,  
BC V6T 1Z4, Canada

of bamboo cycles should determine the degree of nomadism and amplitude of bamboo-specialist population cycles. Nomadism appears to be distributed along a continuum from the temporarily nomad insectivores and mixed strategists to the local and regional nomadic seed specialists. A protected area cannot shelter healthy populations of the most specialized bamboo-seed specialists because they track temporally and spatially unpredictable resources over large temporal and spatial scales. Overall, to effectively protect this ecological system, it is crucial to conserve a network of natural areas capable of providing bamboo in different phases and at different times and places, as well as subsidiary food resources that will allow birds to move away from bamboo patches as they become unsuitable to new, suitable patches.

**Keywords** Bamboo · Cycle amplitude · Cycle length · Masting · Mixed strategist · Population cycle · Pulsed resources · Specialist insectivore · Specialist granivore · Specialization

In much of the Americas, Asia, Oceania, and Africa, populations of a diverse array of bamboo-specialist birds must respond to the growth, masting, and die-off cycles of mass-flowering bamboos. Birds that specialize on bamboo make up a considerable component of tropical and subtropical avifauna, including about 7 % of landbirds at sites in the Peruvian Amazon and the Atlantic forest of Argentina (Kratter 1997; Bodrati et al. 2010). These birds feature prominently on endangered species lists, yet little is known about their biology (Collar et al. 1992, 2001; BirdLife International 2011). In the coming years, conservation of threatened bamboo-specialist birds will depend critically on understanding the relationships between these birds and the strongly fluctuating resources provided by different species of bamboos. Surprisingly, few attempts have been made to understand the population ecology of bamboo specialists, or to predict patterns of occurrence or abundance in time and space. Here, we propose a theoretical framework for understanding the population ecology of bamboo-specialist birds and discuss implications for their conservation.

Bamboo-specialist birds experience extreme variability in their habitat and food sources. Woody bamboos are characterized by clonal (vegetative, asexual) reproduction, facilitating rapid colonization of canopy gaps after large-scale disturbances such as fire and wind, and often generating vast monospecific stands that allow specialist birds to reach high densities (Gadgil and Prasad 1984; Kratter 1997; Gagnon and Platt 2008). Most woody bamboos are long-lived and semelparous, with many years of vegetative growth and a single heavy investment in sexual

reproduction, followed by death (Seifrizz 1920, 1950; McClure 1966; Gadgil and Prasad 1984). Reproductive investment may be incredibly high, providing an abundant source of nutritious food for seed-eating birds. A single individual of *Bambusa arundinacea*, for example, produces up to 68 million flowers, amounting to 3.7 kg of seed per culm (stem), about 30 % of above-ground biomass, or 1 kg seed/m<sup>2</sup> (Gadgil and Prasad 1984). Thus, the life and death cycle of a typical woody bamboo includes a long vegetative phase, a short period in sexual reproduction (seeding), and a short period dead.

Bamboo species vary in synchronicity of sexual reproduction across spatiotemporal scales (Campbell 1985). While some species flower continuously in time, but scattered in space, over different parts of their distribution, others exhibit a single, synchronized masting (mass-seeding) event, followed by mass death over hundreds of square kilometers (McClure 1966; Janzen 1976; Gadgil and Prasad 1984; Campbell 1985; Judziewicz et al. 1999). These masting events can be spatially structured (e.g., a wave from south to north) or chaotic (Gadgil and Prasad 1984; Franklin 2004; Areta et al. 2009), and intermasting intervals vary widely, from 3 to 120 years depending on the species, with most species apparently flowering at 15- to 60-year intervals (Parodi 1955; Janzen 1976; Judziewicz et al. 1999). Thus, in a matter of 1 or 2 years, bamboo-specialist birds may pass from a period of overabundant habitat and food resources to a period of extreme resource scarcity.

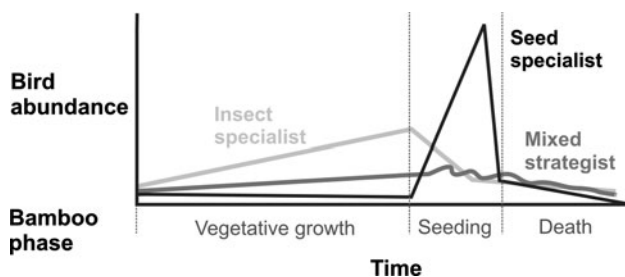
Animals that depend on bamboo face specific challenges and opportunities that depend on the ecology, life-histories, and distributions of the assemblage of bamboos in their community. Sixty-six percent of the ca. 1,500 known bamboo species are distributed in Asia and Oceania, 29 % in the Americas, 2.2 % in Madagascar, and 0.3 % in Africa (Bystrakova et al. 2003, 2004). Up to 142 bamboo species may coexist in a reduced area in south-east Asia and up to 35 species in South America (Bystrakova et al. 2003, 2004). Nevertheless, bamboo specialists may not use all species of bamboos present in their distribution. The Atlantic forest of Argentina, for example, harbors five common species of woody bamboos, but all records of three bamboo specialists, the Purple-winged Ground-dove (*Claravis geoffroyi*), Temminck's Seedeater (*Sporophila falcirostris*) and Buff-fronted Seedeater (*S. frontalis*) from 1957 to 2008 coincided in time and space with masting events of the two common native *Guadua* bamboos (Areta et al. 2009), while the records and the changes in abundance of the Sooty Grassquit (*Tiaris fuliginosa*) are related to the seeding of different bamboo species (Areta and Bodrati 2008). In the Atlantic forest of Brazil, mast-seeding of *Chusquea* aff. *Meyeriana* provided a mass breeding opportunity for the Uniform Finch (*Haplospiza unicolor*)

but not for *S. frontalis* and *T. fuliginosa* (Olmos 1996). In contrast, mass-seeding and die-off of *Merostachys clausenii* at a site in Argentina resulted in strongly reduced detection rates for several bamboo-associated insectivorous birds, including Ochre-collared Piculet (*Picumnus temminckii*), Dusky-tailed Antbird (*Drymophila malura*) and Yellow Tyrannulet (*Capsiempis flaveola*), some of which may have declined regionally, while others moved to alternate species of bamboos at nearby sites (Bodrati et al. 2010). Since the ecology, distribution, and conservation of bamboo specialist birds may be closely linked to specific bamboos, it is important to understand the relationships between bird species and bamboo species (Bodrati and Areta 2006), and to investigate how birds respond to the extreme temporal and spatial variation in bamboo resources.

### Bamboo-specialist strategies

The response of bamboo-specialist birds to bamboo cycles should depend on their diet (Fig. 1). Three main diet and life-history strategies can be identified based on their natural history attributes: insectivore, seed specialist, and mixed strategist.

The first group, insectivorous bamboo specialists, inhabit woody bamboos and may be relatively sedentary during



**Fig. 1** Relationship of abundance through time of three bamboo-specialist types in relation to a bamboo cycle. Population sizes are directly linked to bamboo resource availability. Insectivores will increase over the vegetative phase of bamboo, enjoying long periods of resource availability. They will experience a short period of resource scarcity and decline when bamboos flower and die, assuming that birds specializing in insects that dwell in green bamboo will not be able to cope successfully with a different community of insects using dead bamboo. Seed specialists will face long periods of scarcity during the vegetative phase of bamboo, punctuated by short periods of superabundance of resources when the bamboos flower. They will reach their peak abundance toward the end of the bamboo masting event, as a result of juveniles produced during the mass breeding opportunity provided by the abundant bamboo seeds. Populations of mixed strategists will be more stable, increasing and fluctuating during seeding events (depending on the interaction between an increment in seed supply and a decrease in insect and shoot supply), and decreasing after the die-off

the long vegetative growth phase, but they must experience population declines, switch to alternative habitat, or travel widely during bamboo die-off events. They benefit from long-term habitat stability but must face short-term reductions in habitat that do not affect all generations of birds. Many insectivorous species appear to exist at higher densities and to have smaller territories than non-bamboo-specialists of similar characteristics (Kratter 1997). Insectivorous bamboo specialists are taxonomically widespread and include several species of woodpeckers (Picidae), tyrant flycatchers (Tyrannidae), antbirds (Thamnophilidae), ovenbirds (Furnariidae), babblers (Timaliidae), and others (Short 1973; Parker 1982; Parker et al. 1997; Kratter 1997; Lane et al. 2007; Collar and Robson 2007).

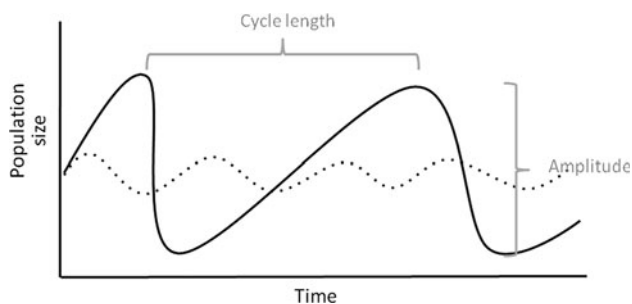
The second group, bamboo seed specialists, must rely on an ephemeral source of food available only after large intervals of time at most locations. For a bird to learn inductively when a (third) bamboo masting event will occur, it would need to attend two previous masting events in the same area. Since bamboo cycles are typically much longer than the lives of individual birds, there is no chance for seed-specialist birds to learn when and where bamboo seeds will be available in the future. Thus, although bamboo seed availability is ecologically predictable (i.e., seeds are always available after the same length of time at a given place), seed availability is unpredictable to individual birds (Areta et al. 2009). During their lifetime, most individual bamboo seed specialists must face a lack of their preferred food supply, at which time they must wander to survive, in a manner typical of nomadic birds that follow ephemeral food resources (Keast 1961; Neudorf and Blanchfield 1994; Dean 1997; Kratter 1997; Sick 1997). Bamboo-seed specialists are only likely to arise in regions with (1) high species richness of bamboos, (2) bamboo species with energetically rewarding seeds that compensate the large costs associated with wandering, and (3) masting events of different bamboos that occur close enough together in time and space to ensure a reasonably continuous seed supply for nomadic birds. Bamboo seed specialists include several species of finches (Thraupidae, Emberizidae, Estrildidae) and doves (Columbidae) (Jackson 1972; Robson 2004; Restall 1995; Areta and Bodrati 2008; Areta et al. 2009).

The third group, mixed strategists, usually feed on bamboo shoots, leaves, and insects, but consume bamboo seeds when available. Their life history combines elements of both previous categories: they can benefit from long-term habitat stability like insectivores, and take advantage of masting events like seed specialists. Mixed strategists include *Amaurospiza* seedeaters, apparently a few *Paradoxornis* parrotbills and the Plushcap (*Catamblyrhynchus diadema*) (Bertoni 1919; Hilty et al. 1979; Sánchez 2005; Robson 2007).

## Degree of specialization and population fluctuations

Among bird species, the degree of specialization on bamboo ranges from opportunistic exploitation to obligate dependence (Jackson 1972; Janzen 1976; Parker 1984; Kratter 1997; Lebbin 2006; Areta et al. 2009). For example, Kratter (1997) categorized bamboo-specialist insectivores at a site in the Amazon as obligate, near-obligate, or facultative bamboo specialists, depending on how often they were found in bamboo habitats and using other habitats locally and over a wider geographic range. The degree of specialization may also vary geographically within a species (Kratter 1993). Partial bamboo specialists will exhibit populations that dwell in bamboo and populations which live away from bamboo stands. Morphologically, some bamboo-specialized populations may be more similar to non-specialist populations than to other specialized populations, which suggests that bamboo specialization may evolve more as a matter of habitat choice and is not linked to bamboo substrate choice (Kratter 1993). Less specialized (partial and facultative) bamboo specialists should be able to cope with bamboo die-offs more easily than more specialized (obligate and near-obligate) species that seem dependent on bamboo stands, and thus should experience less dramatic reductions in habitat availability and relatively minor population fluctuations.

In general, niche width, or its opposite, degree of specialization, should determine the degree of nomadism and amplitude of bamboo specialist population cycles locally and regionally (Fig. 2). Less specialized birds will occupy and breed in a variety of bamboo species, such that asynchronous masting of these different species of bamboos allows relatively stable populations at least at a regional scale (Figs. 2, 3). In contrast, some seed specialists show

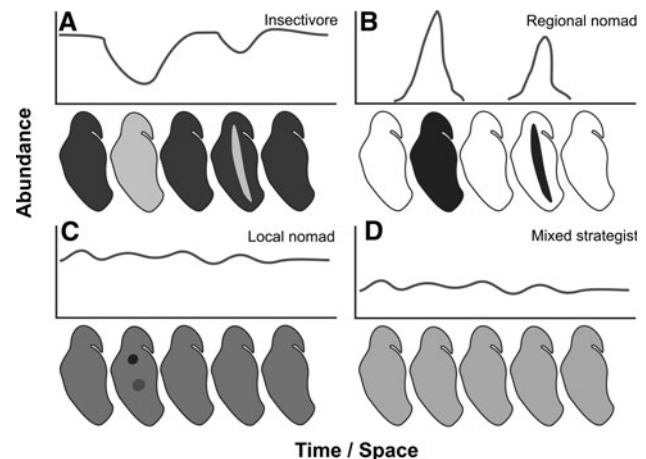


**Fig. 2** Hypothesized population cycles of birds with a high degree of bamboo specialization (breeding restricted primarily to one or two genera of bamboo; *solid line*) and a lower degree of bamboo specialization (live and breed in several bamboo species; *dotted line*). The greater the degree of specialization, the larger the expected amplitude of population fluctuations and the longer the expected cycle length. Note that this figure shows idealized population cycles, but in reality population cycles of bamboo specialist birds are likely to be irregular because they respond to the differing cycles of several bamboo species

strong selection for just one or two genera of bamboos, moving among these bamboos at a regional scale and apparently restricting most breeding to masting events (Areta et al. 2009). These extreme specialists are expected to experience high amplitude of population cycles, locally and regionally (Figs. 2, 3).

## Degrees and types of nomadism

Bamboo specialists display varying degrees of nomadism depending on their life-history strategies. Insectivores and mixed strategists are mostly sedentary, but may become nomadic or switch to alternate habitats after bamboo die-offs (Fig. 3). Bamboo-seed specialists, in contrast, are highly nomadic. Their degree of nomadism varies positively with their degree of specialization, and it may vary geographically according to bamboo community composition.



**Fig. 3** Expected abundance (*graphs, above*) and geographic distribution (*maps, below*) of four bamboo specialist bird species in relation to bamboo mastings over a relatively large area of the species' distribution. *Increasingly dark colors on the maps indicate increasing abundance of birds in the area.* **a** Insectivore: populations will decrease in size regionally if a preferred bamboo dies massively; however, the total disappearance of the birds from the area is not expected. Less specialized insectivores may remain at similar abundance throughout the region by colonizing suitable patches of other bamboos. **b** Seed specialist regional nomad: populations will experience large fluctuations in space and time, strictly dependent upon seed availability of one or a few bamboo species; birds will completely vacate the area (or occur at extremely low density) when none of their preferred bamboos are seeding. **c** Seed specialist local nomad: although total population size may not change significantly, large numbers may concentrate at major seeding events (*darker spots in map*), whereas lower density populations may be spread throughout the area (*uniformly colored area in map*) when there are no major seeding events. **d** Mixed strategist: widespread low-density populations will be more or less evenly distributed through time and space. Even if local increases in population numbers occur due to bamboo-masting triggering opportunistic seed-exploiting behavior, these are unlikely to include a large proportion of the total population

We can think of nomadism as distributed along a continuum between local nomads and regional nomads. Local nomads use resources that are always patchily available over a relatively small area in such a way that they can be found year-round every year making use of the resources and breeding accordingly (Fig. 3). Regional nomads use resources that occur patchily in time and space over a large area in such a way that they are only found in the area when the resource is available but then vacate the area for long periods of time, travelling large distances (Fig. 3). The bamboo setting in the total geographic range of these birds will condition their abundance in different parts of their range. Generally, regional nomads would be more specialized than local nomads, exploiting fewer bamboo species.

Nomadism should result in the frequent mixing of ‘populations’ and would consequently tend to impede their evolutionary differentiation. Indeed, the concept of a spatially and temporally secluded population is almost inapplicable to the most nomadic bamboo-seed specialists. As a result of nomadism and the stringent requirements for bamboo-seed specialization to evolve, the number of bamboo-seed specialist species is well below that of insectivorous specialists. For the most nomadic birds, the total geographic range will hardly ever be occupied simultaneously by birds; since they are nomadic, they are never more or less evenly spread over the whole range but occurring only in parts of it at any given instant of time (either at high densities during bamboo mastings or in transit between them). In contrast, most insectivores will be present in their whole range simultaneously.

### **Bamboo mastings as attractors of limited power and range**

The specific combination of bamboo species in any locality will exert a strong influence on the temporal and spatial pattern of presence of bamboo specialists locally and regionally. Since seed specialist birds cannot predict when and where seeds will be available, they will presumably wander with no predetermined direction, but with the goal of finding seeding bamboos. Thus, we can think of bamboo masting events as attractors of bamboo-seed specialist birds. While niche width can be considered a proximate determinant, the bamboo reproductive cycles, bamboo species richness in a given area, and the spatial distribution of bamboo stands can be considered ultimate determinants of nomadism in bamboo specialists.

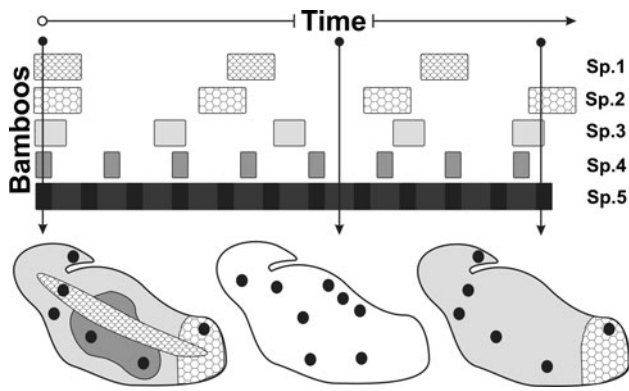
These attractors do not play an absolute role, they do not act independently of other mastings and are thus not capable of ‘sucking in’ all birds. Instead, they would attract a certain number of birds depending on the specific features of a bamboo (masting size, temporal and geographic

seeding pattern, seed size and type, etc.), the aptitude of a bird to exploit it (bill size and shape, foraging maneuvers, vagility, etc.), and the number of birds present in the region due to chance or to the effects of previous mastings. In sum, the bamboo-masting events, unpredictable to individual birds, are non-absolute attractors of limited power and range. For example, large masting events may go unnoticed by seed specialists, not because the bamboo is unsuitable, but because another masting event may be occurring simultaneously at a distant location. On the other hand, two masting events occurring at the same distance from a central point would be mutually exclusive alternatives for the regional pool of birds. Conversely, the absence of any masting event nearby may prompt seed specialists to feed upon alternative food sources as they search for seeding bamboo patches. Indeed, bamboo-seed specialists must necessarily occur away from bamboo habitats when wandering in search of suitable seeding bamboos (Lentino and Restall 2003; Areta et al. 2009). Thus, wandering outside of bamboo habitat is an essential feature of bamboo-seed specialists and not evidence against their specialization (e.g., Sánchez et al. 2006; see also Kratter 1997 for insectivores). In this sense, areas where birds use alternative food sources may be considered as areas that fall outside the field of attraction of a seeding bamboo patch.

### **Long-term dynamics of bamboo cycles at a community scale**

Although most species of bamboos experience regular cycles of vegetative growth, masting, and die-off, species differ in cycle length, masting duration, timing, and synchronicity over space. At a community level, then, bamboo species are out of phase with each other. Masting events of several bamboo species may coincide one cycle, but not the next. This lack of phase is important for bamboo specialists because it will result in a temporal and geographic mosaic of resource availability over very long periods of time, where the initial conditions that any bird experienced may occur only sporadically over centuries and very large regions. Depending on the exact composition of bamboos in a community, some flowering-overlap events may occur more often than others (Fig. 4).

Changes in bamboo phase overlap will have varying effects on populations of bamboo-specialist birds, depending on their life-history strategy and degree of specialization. Populations of insectivores and mixed strategists may crash if all alternative bamboo habitats have died, or they may persist at very low numbers if only one suitable bamboo species remains in the vegetative phase. Seed-specialist local nomads will experience quasi-cyclical



**Fig. 4** Long-term dynamics of bamboo-flowering overlap. Hypothetical sequence of flowering overlaps for five bamboo species starting at a point in time where all the bamboo species flower simultaneously. Duration of each flowering event for each bamboo species is indicated by the *width* of the corresponding *block* and intermasting period by the *space* between two successive *blocks*. Different patterns of geographic distribution of flowering bamboos (*maps*) will occur at different points in time (*vertical arrows*). Bamboo species 1–4 each flower fairly synchronously over their distribution, while species 5 flowers periodically at a given locality but patchily over a large area and continuously over time at the shown scale (*continuous bar*); note the coincidence in geographic pattern of flowering of species 5 in the *left* and *right maps*, which differ from the pattern shown in the *middle map*

periods of abundance and scarcity of resources, but will maintain overall population numbers provided that any bamboo is seeding. For seed-specialist regional nomads specializing on one or a few bamboos, changes in phase overlap may condition their ability to reach their remote preferred food sources. For example, seeds of non-preferred bamboos may facilitate long-distance movements by acting as stepping-stones between preferred bamboos, but their availability between masting events of preferred bamboos will depend on the cycles of the non-preferred bamboos. The local availability of alternative bamboo food sources may also allow for the sustained persistence of bamboo seed specialists in an area after a masting event of the preferred bamboo is over, but this may or may not occur during a second masting of the same preferred bamboo. Moreover, the preferred bamboos may flower in an alternate fashion reducing periods of seed scarcity, but if bamboo cycle-lengths differ, the bamboos will occasionally flower at the same moment and a long period of resource scarcity will follow. Thus, the individual unpredictability of resource availability for seed-specialists is further complicated by the differences in cycle length and consequent changes in phase overlap between different species of bamboos (Fig. 4). This ecological predictability (stemming from the clock-like flowering behavior of masting bamboos), but individual unpredictability (stemming from the short life-span of individuals in relation to intermasting periods), should be taken as a landmark of

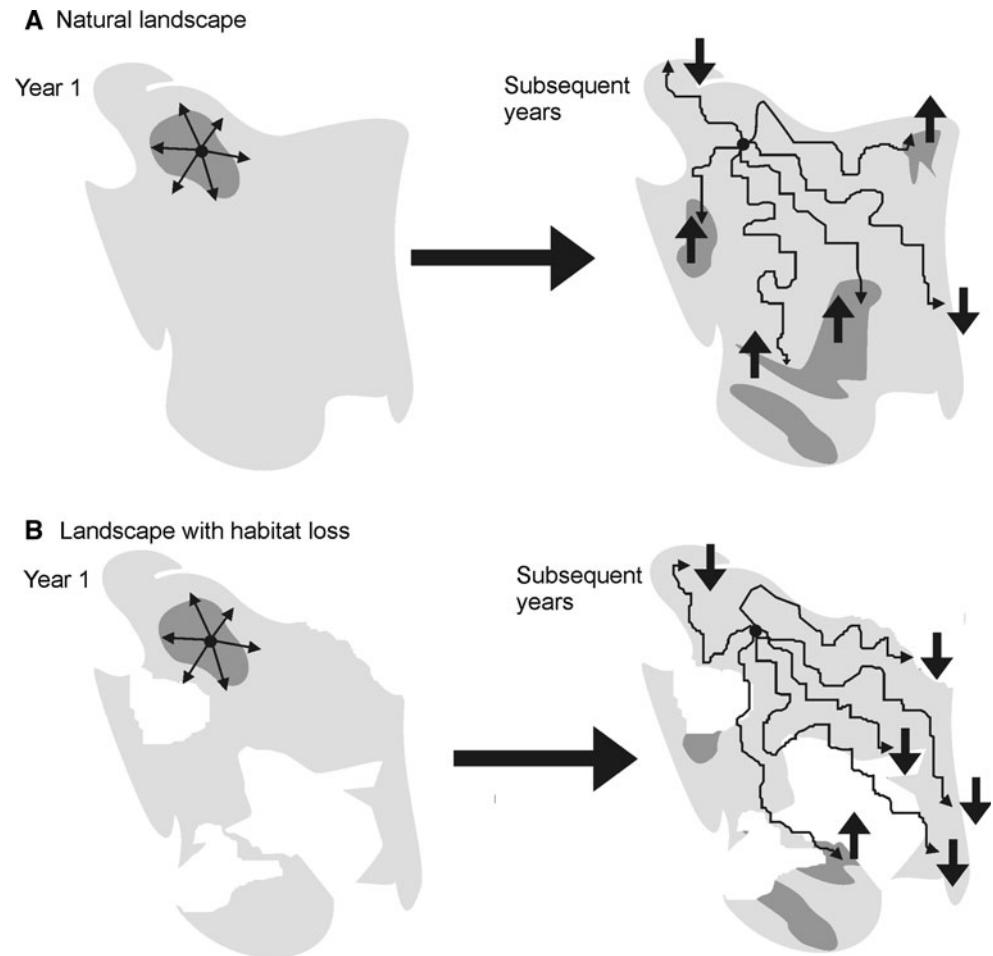
bamboo-seed specialists and as the most basic principle for understanding their ecology.

### The conservation challenge

Population cycles of bamboo-specialist birds make these species particularly vulnerable to extinction, and conservation and monitoring strategies are urgently needed that take into account the natural fluctuations in abundance and distribution of these birds. The most critical period for these populations is the period of resource/habitat scarcity; i.e., for insectivores when the bamboo dies, and for seed specialists when few or no bamboos have seeds. The most specialized bamboo users should experience the largest fluctuations and be the most vulnerable to extinction. For conservation purposes, we recommend a long-term, conservative approach to estimating population size and abundance trends for the most specialized bamboo seed specialists. Observations of thousands of individual seed specialists co-occurring simultaneously after a mass breeding event in a large seeding stand of bamboo at one place and time should not be taken to indicate that the species is always abundant or that the population is increasing over the long term. Populations of mass-breeding seed specialists will naturally increase very quickly in the short term, but they will also naturally decline over long periods of resource scarcity with few breeding attempts as they disperse in search of suitable bamboo patches. Thus, large population numbers may be necessary to guarantee the arrival of a few individuals to suitable seeding bamboos; populations may crash if they fall below a certain threshold that does not allow for a new demographic explosion and consecutive mass dispersal.

We also recommend a conservative approach in protecting habitat for bamboo specialists. Short-term datasets are insufficient to determine area requirements, because they do not incorporate the dynamic nature of bamboo habitat availability, and measures deemed adequate for other organisms (such as protecting 15 % of a region as native habitat) will often be insufficient for bamboo specialists. Given the large fluctuations of bamboo resources in time and space, long-term conservation success will rarely be achieved by protecting a single area. A relatively large reserve with many species of bamboos may be able to effectively preserve a population of a less specialized bamboo specialist. However, as nomadic birds, seed specialists will traverse in large numbers the limits of the protected area or will make effective use of the reserve only sporadically when seeds are available. A protected area cannot shelter healthy populations of the most specialized bamboo seed specialists because these species track temporally and spatially unpredictable resources over

**Fig. 5** Hypothesized fate of bamboo specialist populations in a forest landscape under two scenarios. *Light gray* represents native forest, *dark gray* suitable bamboo patches. **a** Under natural conditions (no anthropogenic habitat loss), birds disperse in all directions (*thin arrows*) when the bamboo patch becomes unsuitable (end of *Year 1*). In subsequent years, they wander nomadically. Many find other suitable bamboo patches, breed, and their populations increase (*thick upward arrows*). Others do not find a suitable bamboo patch, do not breed, and their populations decline or disappear (*thick downward arrows*). **b** In a landscape where forest has been cleared (habitat loss), birds again disperse in all directions at the end of *Year 1* when their bamboo patch becomes unsuitable. In subsequent years, they again wander nomadically, but now a much lower proportion of individuals find suitable bamboo patches, such that most populations decline or disappear. Thus, the habitat-loss scenario results in regional population decline and an increased risk of extinction



large temporal and spatial scales. The high vagility of the most extreme bamboo seed specialists may render these species relatively robust to habitat fragmentation. However, because many resource patches are required to support a single individual over time, and because alternative food sources may play a key role when bamboo seeds are lacking, these species might be highly vulnerable to habitat loss of both their preferred bamboo stands and the intervening areas with alternative food sources (Fig. 5). To conserve bamboo specialist birds in the long term, it is critical to conserve enough bamboo habitat, and with enough connectivity, that at least some of the birds dispersing from a formerly suitable bamboo patch will find another suitable patch elsewhere. Insectivorous birds and mixed strategists need to be able to move consistently from dying bamboo patches to living patches, and seed specialists need to move from dying bamboo patches to seeding patches. Thus, generally, availability of suitable habitats for insectivorous and mixed strategist birds spe-

cializing on bamboos will be inverse to that of bamboo seed specialists (Fig. 5). Overall, to effectively protect this ecological system, it is crucial to conserve a network of reserves or natural areas capable of providing bamboo in different phases and at different times and places, as well as subsidiary food resources that will allow birds to move away from bamboo patches as they become unsuitable, to new, suitable patches.

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