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Research Letter

A Constraint-based model of Dynamic Island Biogeography: environmental history and species traits predict hysteresis in populations and communities

Joseph R. Burger[1,2,3*], Robert P. Anderson[4,5,6], Meghan A. Balk[7,8] and Trevor S. Fristoe[9,10]

[1] Department of Biology, University of North Carolina, Chapel Hill, North Carolina USA

[2] Duke University Population Research Institute, Durham, North Carolina USA

[3] Institute of the Environment, University of Arizona, Tucson, Arizona USA (present address JRB)

[4] Department of Biology, City College of New York, City University of New York, New York, New York USA

[5] Program in Biology, Graduate Center, City University of New York, New York, New York USA

[6] Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History, New York, New York USA

[7] Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia USA

[8] Bio5 Institute, University of Arizona, Tucson, Arizona USA (present address MAB)

[9] Department of Biology, Washington University in St. Louis, St. Louis, Missouri USA

[10] The Ecology Group, Department of Biology, University of Konstanz, Konstanz, Germany (present address TSF)

*Corresponding author: ecoevoburger@email.arizona.edu

Abstract. We present a conceptual model that shows how hysteresis can emerge in dynamic island systems given simple constraints on trait-mediated processes. Over time, many real and habitat islands cycle between phases of increasing and decreasing size and connectivity to a mainland species pool. As these phases alternate, the dominant process driving species composition switches between colonization and extinction. Both processes are mediated by interactions between organismal traits and environmental constraints: colonization probability is affected by a species' ability to cross the intervening matrix between a population source and the island; population persistence (or extinction) is driven by the minimum spatial requirements for sustaining an isolated population. Because different suites of traits often mediate these two processes, similar environmental conditions can lead to differences in species compositions at two points of time. Thus, the Constraint-based model of Dynamic Island Biogeography (C-DIB) illustrates the possible role of *hysteresis*—the dependency of outcomes not only on the current system state but also the system's history of environmental change—in affecting populations and communities in insular systems. The model provides a framework upon which additional considerations of lag times, biotic interactions, evolution, and other processes can be incorporated. Importantly, it provides a testable framework to study the physical and biological constraints on populations and communities across diverse taxa, scales, and systems.

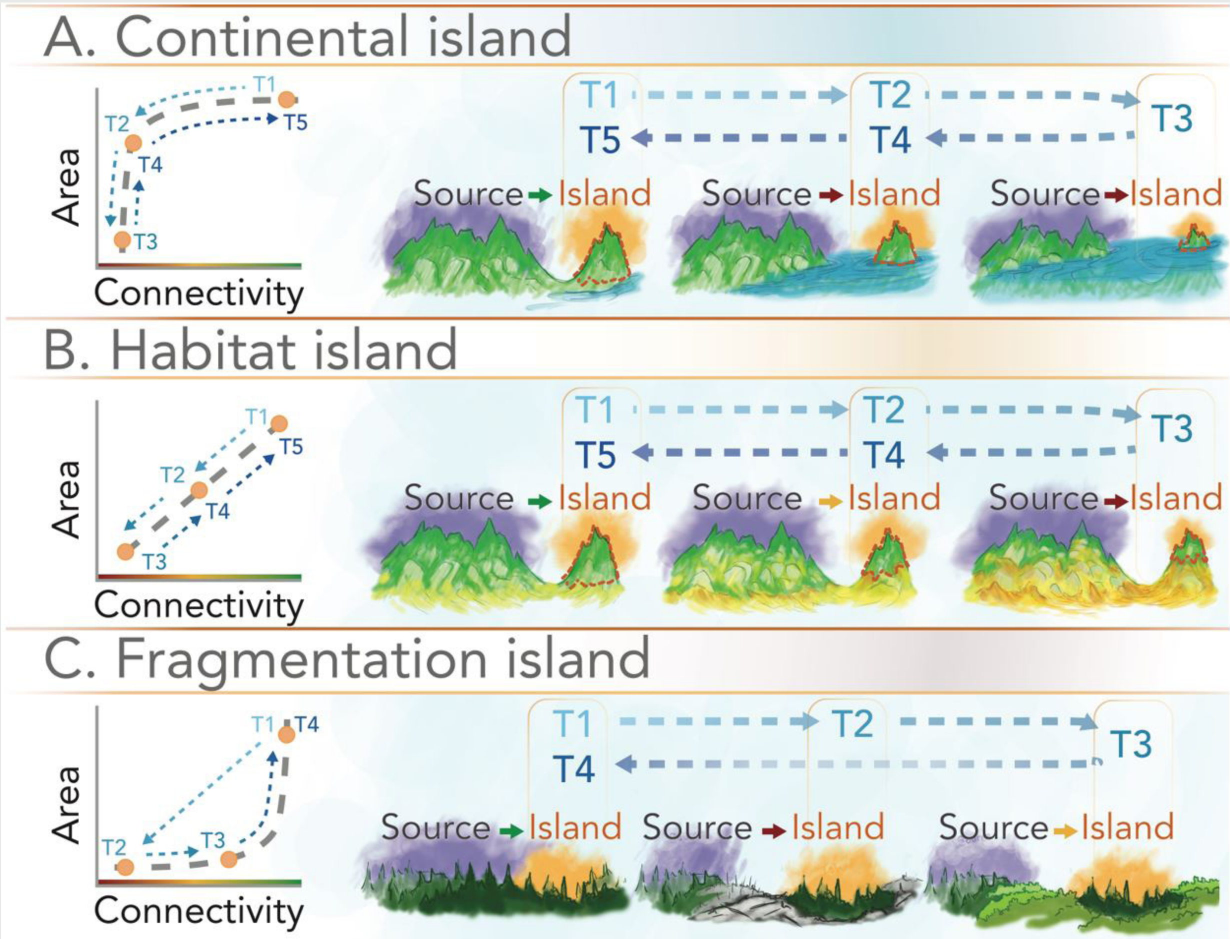
Keywords: Colonization, Constraints, Environmental Cycles, Extinction, Immigration, Metacommunity, Metapopulation, Minimum Viable Population, Multiple Stable States, Niche

Introduction

The Earth is dynamic and many natural systems cycle in predictable ways. Landscapes change over space and time, resulting in patches of habitats that expand and contract, appear and disappear, connect and disconnect. For example, cycles of variation in the Earth's orbit identified by Milutin Milankovich drive global climate change over geological time scales (Jansson and Dynesius 2002). Throughout the

Pleistocene, these cycles caused repeated sea-level changes as well as latitudinal and elevational shifts in climate, creating archipelagos of real (e.g., continental islands) and habitat islands (e.g., mountaintop 'islands') that changed through time (see Box 1a and b). Over shorter time scales, natural and anthropogenic forces shape similar cycles as habitat patches are alternately fragmented and united by disturbance and succession (Box 1c). As fundamental features of the planet, these cyclical and predictable changes have arguably played a major role in affecting species distributions, population and community composition, and the generation and maintenance of biodiversity.

Such environmental change in continental islands and habitat patches can alter both island size as well as connectivity to larger contiguous areas of



Box 1. Examples of island systems that undergo cyclical environmental changes and their predicted dynamics of size and connectivity.

A) Continental or landbridge islands, B) Habitat islands (e.g., sky islands or other refugia of isolated habitats), and C) Fragmentation islands. The dashed blue arrows show the temporal progression of the system through environmental cycles. Islands are highlighted (or outlined) in orange and the mainland source in purple. The arrows connecting source to island are colored based on current island connectivity.

Environment change drives cyclical variation that influences area and connectivity. For example, continental islands (A) form as they are isolated by rising sea level, followed by a gradual period of extinction as the island progressively shrinks towards inundation. Afterwards, connectivity is reestablished once the mainland is connected, allowing rapid colonization. In contrast, habitat islands (e.g., sky islands (B)) are isolated by varying degrees of environmental gradients, and long-term climatic cycles (e.g., glacial–interglacial) cause gradual changes in both area and connectivity. Gradual phases of extinction and colonization alternate, tracking environmental change. The system cycles repeatedly in a predictable way, although the duration and amplitude of each phase may vary. Lastly, in fragmentation islands (C), over short time scales natural or anthropogenic disturbances isolate habitat patches, which may eventually reconnect to contiguous areas of similar habitat as succession occurs within the intervening matrix. An initial wave of extinction accompanies a rapid decrease in area and connectivity. If the matrix recovers, a slower period of recolonization will occur as area and connectivity gradually increase. In different systems, cycles may occur repeatedly and predictably depending on the cause and duration of disturbance. While these and many systems will show covariation in island size and connectivity, such concordance is not necessary for the model to make predictions.

similar habitat (i.e., the mainland). As these systems undergo environmental cycles, changes in the insular community composition are dominated by two distinct phases: i) colonization leads to higher species richness during periods of increasing connectivity as the intervening matrix separating an island from the mainland becomes shorter and/or easier to traverse; and ii) extinction reduces species richness during periods of decreasing area as an island's capacity to support populations declines (Box 1). The importance of these two processes was central to MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography (ETIB), which made predictions for the equilibrium species richness on environmentally static islands with dynamic immigration and extinction. Recent extensions have incorporated the dynamic nature of oceanic island environments to explore how island progression through birth, growth, decay, and re-submergence affects biological communities (Heaney 2000, Heaney 2007, Whittaker et al. 2008, Warren et al. 2015, Weigelt et al. 2016, Lenzner et al. 2017, Whittaker et al. 2017). In parallel, a surge of studies has begun to incorporate trait-based approaches for studying ecology and biodiversity (e.g., McGill et al. 2006, Violle et al. 2014, Enquist et al. 2015) and community assembly (Shipley et al. 2006, Shipley 2010, Shipley 2015, and Vellend 2016). Yet, a complete picture of how trait-mediated constraints influence species distributions on dynamic islands, in particular those that undergo cyclical change, remains elusive.

To fill this void, we present a conceptual model describing how the environmental cycles that drive island dynamics can shift the ecological constraints that influence colonization and extinction. Recent extensions of the classic ETIB have begun to identify how differences in functional traits can mediate colonization and extinction processes (Kirmer et al. 2008, Laurance 2008, Okie and Brown 2009, Vellend 2016, Jacquet et al. 2017, Leibold & Chase 2018). We build on this work by incorporating the interactions of key functional traits with dynamic environmental constraints to predict species composition in insular systems. Our model predicts a possible role of *hysteresis*—the dependency of outcomes not only on the current system state but also the system's history of environmental change—in shaping the biodiversity of dynamic island systems. Specifically, we demonstrate how the distribution of populations and community composition can depend not only on the current system state but also on the history of environmental cycles. Hysteresis has been identified as an emergent property of many complex systems, such as in the context of multiple stable ecosystem states (Scheffer et al. 2001, Sternberg 2001, May et al. 2008, Scheffer 2009, Scheffer et al. 2009, Hirota et al. 2011). Leveraging the cyclical nature of certain insular systems may provide a powerful way to understanding how hysteresis in complex ecological systems can emerge from simple constraints on species functional traits (Chase 2003, Fukami and Nakajima 2011).

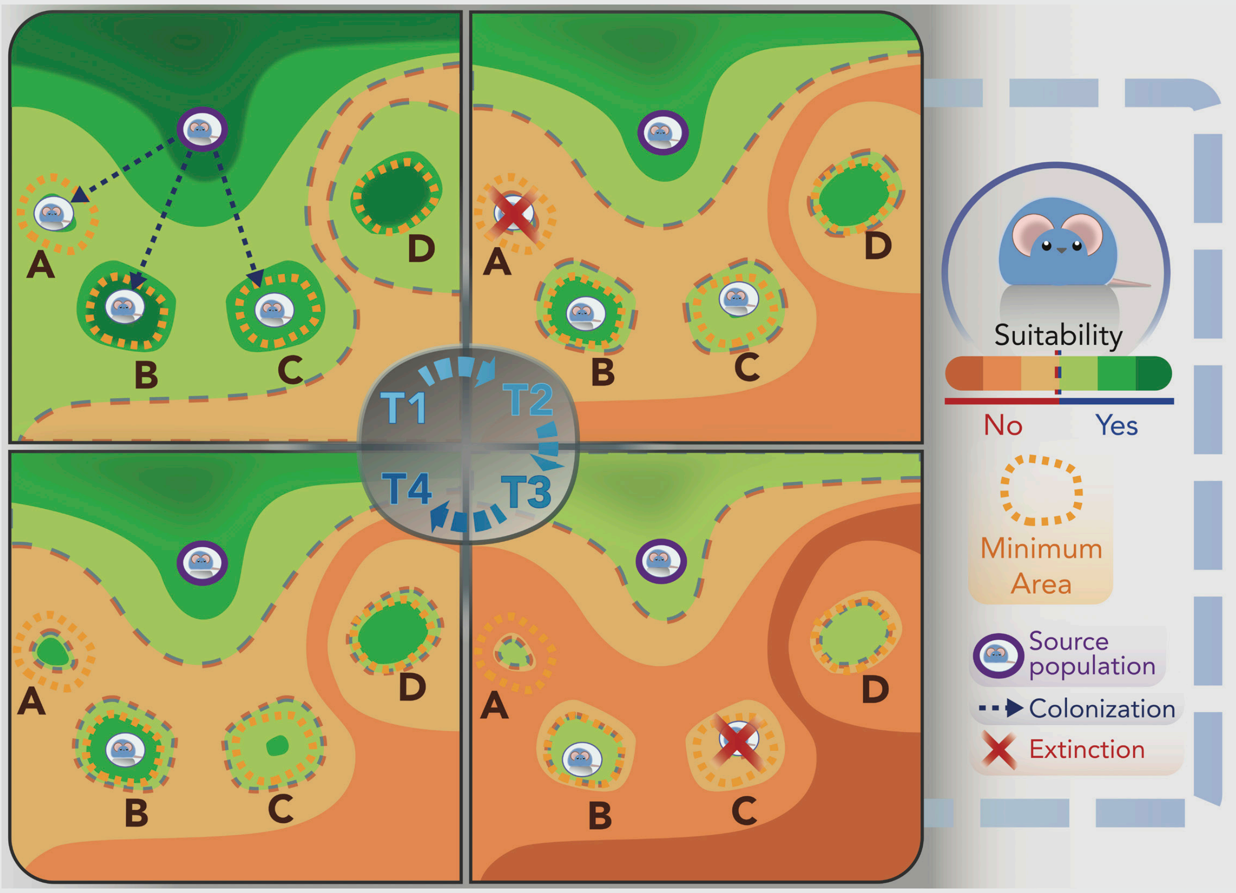
A Constraint-based model of Dynamic Island Biogeography

Here we present a Constraint-based model of Dynamic Island Biogeography (C-DIB) that combines the dynamic nature of island size and connectivity with trait-based constraints on colonization and extinction. The model predicts the presence or absence of populations for a given species at any temporal point along environmental cycles (Box 2: Single species model). When applied across all species within the mainland source pool, the model predicts an island candidate species pool – the set of species available for local community assembly (Box 3: Community model). We begin with a straightforward conceptual model that deliberately makes simplifying assumptions regarding time lags, biotic interactions, evolutionary stasis, and other important biological processes. We conclude with suggestions for further evaluation of the C-DIB through empirical testing and simulation studies, which should provide insights into the context-dependent roles that these additional biological realities play.

Colonization

The probability of species colonization has classically been linked to traits that constrain individual dispersal ability (MacArthur and Wilson 1967). The capacity for flying, rafting, or drifting facilitates crossing barriers and corresponds to quantifiable traits such as wing loading in birds (Hamilton 1961), swimming ability in terrestrial mammals (Meijaard 2001), and cluster size in seeds (Seidler and Plotkin 2006). Similarly, traits such as body size and home range are indicative of dispersal distance in terrestrial mammals (Bowman et al. 2002), and experimental behavioral tests have shown that variation in willingness to traverse open areas can explain colonization patterns in forest birds of insular systems (Moore et al. 2008). In addition to such individual-level processes, the establishment of populations across a matrix via corridors and stepping-stones can be a primary means of colonization (Baum et al. 2004). At one extreme, the matrix separating islands from the mainland can be entirely inhospitable. For example, the saline ocean that isolates continental-shelf islands is physiologically intolerable to most amphibians. However, in many other insular systems, the barriers separating patches from nearby areas of contiguous similar habitat are less discrete (Laurance 2008, Prevedello and Vieira 2010). These intervening regions can be viewed as semi-permeable, with suitability varying among species depending on their dispersal capacity and demography in the conditions throughout the matrix (Lomolino 1993, Åberg et al. 1995, Stouffer and Bierregaard 1995, Keymer et al. 2000, Grayson 2006, Waltari and Guralnick 2009). Conceptually, island connectivity can be quantified as the environmental similarity of conditions in the matrix compared with those found on the island, with high connectivity relating to higher overall probabilities of colonization (Prevedello and Vieira 2010). Colonization is further influenced by species-specific tolerances to the matrix conditions. Information on natural history (e.g., Brown, 1971) and physiological limits (e.g., Kearney and Porter 2009) in combination with ecological niche modeling (Peterson et al. 2011, Soley-Guardia et al. 2016, Kass et al.

Box 2. The Constraint-based model of Dynamic Island Biogeography illustrated for populations of a single hypothetical species over space and time.



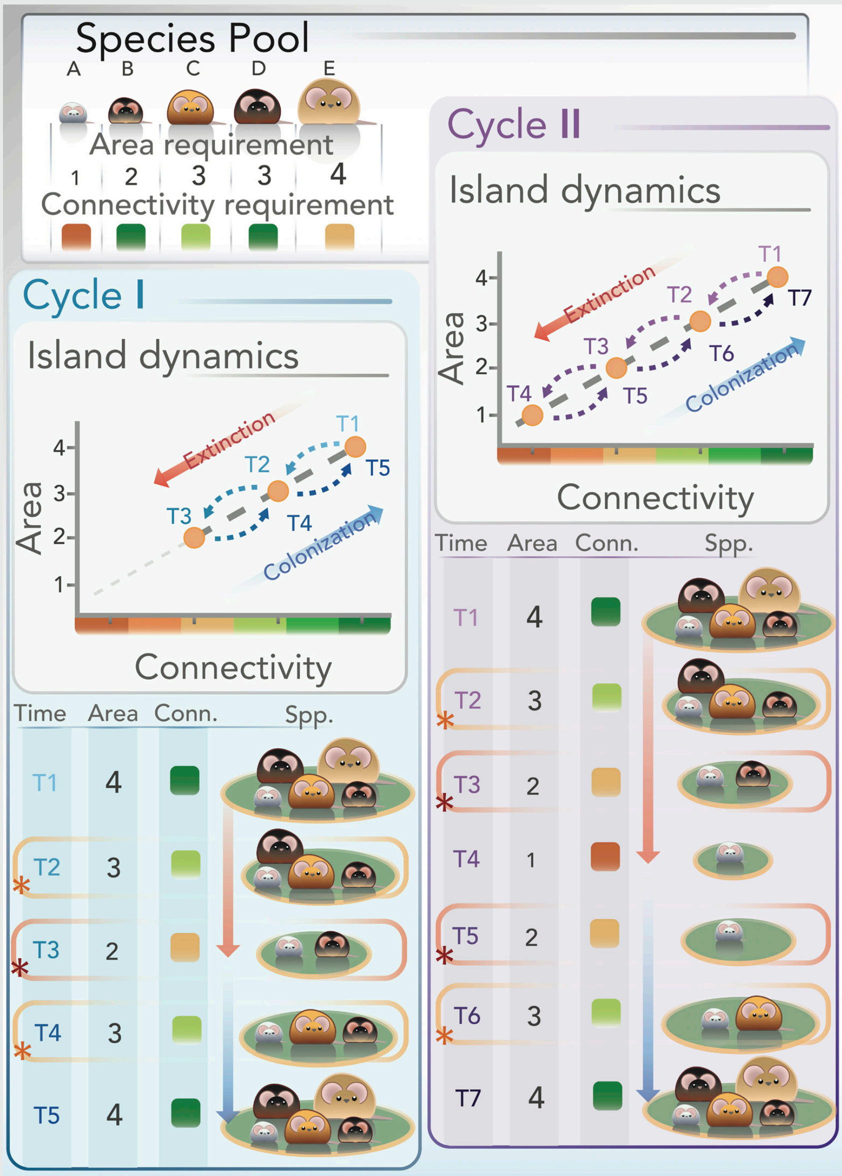
Consider a landscape where climatic shifts and associated cycles of glaciation create a series of dynamic mountaintop islands of suitable mesic forests (green areas) among vast unsuitable desert habitat in the lowlands (brown areas). During cooler, wetter glacial periods (T1), the islands of forest habitat are large and the low valleys that separate them from the 'mainland' forested mountain range (top of each frame) are relatively mesic. This allows populations to colonize (dark blue dotted arrows) islands A, B, and C. As the climate warms during an interglacial period, the area of suitable habitat will contract as cooler and wetter climates associated with mesic forests recede to higher elevations. The intervening valleys become hotter, drier, and less suitable (T1 –> T3). Over this period, populations will become extirpated from islands that have contracted to become smaller than the minimum area necessary to support a viable number of individuals (e.g., islands A and C). As the cycle continues (T3 -> T4), some islands will regain suitable habitats large enough to support populations. Despite having sufficient suitable habitats, re-colonization will not occur because the intervening matrix is not suitable (T4, islands C and D). Moreover, the area of suitable conditions on island A remains too small. At time T4, the species is only expected to occur on island B where a period of suitable conditions for colonization was followed by a continuous period of island size above the minimum threshold to support a viable population. At T2 and T4, the system shows *hysteresis* – where due to previous environmental conditions the species is distributed on different islands despite identical current conditions.

2018) and landscape resistance models (Howell et al. 2018) can inform measures of environmental suitability that indicate how colonization probabilities vary among species (Collinge 2000, Hunter 2002).

Extinction

The persistence of species on islands is tied to the capacity of the island to support viable populations. In general, because larger islands can sustain a greater number of individuals, the probability of extinction decreases with island size. Hence, larger islands generally have higher species richness (MacArthur and Wilson 1963, 1967). As an island shrinks due to environmental change, extinction is predicted to affect species differently depending on organismal traits that influence the area necessary to support a minimum viable population (Shaffer 1981, Soulé 1987). Indeed, body size and trophic level have been associated with differential extinction risk among island species (Brown 1971, Oksanen et al. 1981, Patterson 1987, Lessa and

Box 3. The Constraint-based model of Dynamic Island Biogeography illustrated for communities over two environmental cycles varying in magnitude.



Consider a single isolated mountaintop habitat island and a suite of species associated with mesic forests to different degrees. As the environment is altered by climatic shifts associated with glacial cycles, the island changes size and is isolated to varying degrees by arid, non-forested areas. Because of species-specific environmental tolerances, each species requires a different level of island connectivity to colonize across the matrix. Moreover, differences in body size lead to interspecific differences in the minimum island area necessary to support a viable population (see species pool 'trait key' in top left). This example progresses through two environmental Cycles (I and II) that both start during a period of high connectivity, when the island is inhabited by the full set of forest-restricted species found on a 'mainland' mountain range.

During these cool, wet glacial periods (e.g., T1 in Cycle I and II), the island of forest habitat will be large and the low valleys that separate it from the mainland range will be relatively mesic. As the climate warms during an interglacial period, the forest habitat contracts as moist climates recede to higher elevations while the intervening valleys become warmer and drier (e.g. T1 -> T3 in Cycle I). Over this period, species will be lost to extinction as the island's size decreases. Traits influencing the area required for sustaining a viable population will dictate the order in which species disappear. In this case, we consider body size and assume that larger species require larger islands. Transitioning back towards a glacial period causes the climate to cool, and the island once again increases in size, restoring the capacity to support all of these mesic-forest species (T3 -> T5 in Cycle I). However, the likelihood of recolonization will depend on the ability of each species to traverse the intervening matrix between island and mainland. In the case of these species, connectivity across the low-lying valleys at a given time is determined by tolerance to arid conditions. Following the environmental cycles demonstrates the role of hysteresis in impacting community composition. In T2 and T4 of Cycle I, *identical* island conditions are associated with *different* species. This is because the composition of species is influenced not only by the current environmental state but also the historical trajectory in the glacial cycle.

The added influence of the magnitude of earlier environmental cycles is evident in Cycle II. After experiencing a particularly warm interglacial period and very small island size (T4 Cycle II), the system returns to intermediate conditions (e.g., T6 in Cycle II). However, the compositions of species present on the island in T5 and T6 in Cycle II are novel for those environmental conditions. They differ from those of any other time period with the same environmental conditions in either environmental cycle. The asterisks (orange: times T2 and T4 in Cycle I and T2 and T6 in Cycle II; red: times T3 in Cycle I and T3 and T5 in Cycle II) indicate island communities that exhibit hysteresis, where *identical* environmental conditions are characterized by *different* communities due to environmental history.

Farina 1996, Marquet and Taper 1998, Crooks 2002, Okie and Brown 2009, Holt 2009, Boyer and Jetz 2014, Crooks et al.2017). In mammals, these traits are known to be strongly linked to individual resource requirements, space use, and population density (Damuth 1981, Silva and Downing 1995, Carbone and Gittleman 2002, Marquet 2002). Additionally, larger islands tend to contain a greater diversity of habitats and resource types, allowing more specialists to occur, whereas smaller islands should feature a higher proportion of generalists (Brown 1971, Okie and Brown 2009). Body size and trophic level are conveniently quantifiable traits (including from fossils). These can be incorporated into allometric scaling relationships to make general predictions of species resource and space requirements to inform extinction probabilities (Marquet and Taper 1998, Ritchie and Olff 1999, Shipley et al. 2006, Okie and Brown 2009, Ritchie 2010, Shipley 2015).

Predicting population dynamics of single species

The C-DIB indicates how in dynamic insular systems, organismal traits such as those outlined above interact with changing environmental constraints to affect species presence and absence. Because different suites of traits often mediate the likelihood of successful colonization and the avoidance of extinction, the presence of a population of a given species on a particular island depends not only on current conditions but also on the history of the system. An island population will become extirpated if environmental change reduces the area of suitable habitat below the minimum threshold necessary to support a viable number of individuals (Marqut and Taper 1998, Mouquet and Loreau 2003, Stephens 2016). Even if future environmental change restores conditions to a sufficiently large suitable area, a population will only reestablish if matrix conditions (i.e., distance or matrix composition) become amenable for colonization. Hence, a species can be absent from an island that it previously inhabited, even when current conditions are favorable for supporting a population (e.g. Box 2, time T4, islands c and d). While previous work on alternative stable states in ecology has typically considered changes at the ecosystem level (e.g., Sternberg 2001, Scheffer et al. 2001, May et al. 2008, Scheffer 2009, Hirota et al. 2011), the outcomes described here for insular systems essentially provide illustration of alternative stable states at the population level. For example, reversing the environmental change for a particular island species (e.g., that leading to extinction) will not necessarily result in reversion to the original state (e.g., re-colonization). This hysteresis in the system is contingent on the trajectory of environmental cycles. A species is only expected to occur in patches that have experienced conditions favorable for colonization, followed by a continuous period where island area is maintained above the minimum required to support a viable population (e.g. Box 2, T4, island b). The C-DIB additionally predicts the absence of species on current patches with sufficiently large areas, providing that past levels of connectivity were not suitable for colonization to occur.

Predicting candidate species pools for local community assembly

The C-DIB also provides insights into how retracing the history of colonization and extinction for each species within the mainland source pool predicts the candidate species expected to occur in the local insular community. Combining the expectations for various individual species following the logical model presented above makes the novel prediction of asymmetrical change in island community composition due to the trajectory of environmental cycle (Box 3: community model; see also predictions in Box 4). The most recent species to go extinct during a period of decreasing island size and connectivity will not necessarily be the first to recolonize when the island system reverses its trajectory and returns to earlier environmental states. Thus, an island can exhibit *identical* area and connectivity to the mainland at distinct points in time but host *different* sets of species (e.g. Box 3, times T2 and T4 in Cycle I and T2 and T6 in Cycle II; or times T3 in Cycle I and T3 and T5 in Cycle II). In operational terms, the candidate species expected for local community assembly on an island will depend on: i) current island conditions (the environmental position in the cycle), ii) the trajectory of recent environmental change (the current phase of the cycle; see Box 3, environmental Cycle 1), and iii) the magnitude of environmental change that occurred during previous cycles (see Box 3, environmental Cycle 2).

Model generality: Functional traits and island types

The C-DIB model should apply generally to a wide range of taxa, island systems, and to environmental cycles that occur over various timescales. The functional traits that mediate colonization and extinction in each system may differ depending on taxa and island type. Natural history knowledge of the system and taxa studied should guide selection of the most informative and useful traits in implementing the model. For example, the barriers separating any type of island from the source or mainland populations can relate to a wide range of environmental filters—including gradients in temperature, soil acidity, vegetation type, ocean depth, or degree of fragmentation (Prevedello and Vieira 2010). In each case, different organismal traits (e.g., thermal physiology, pH tolerance, soil or habitat preference) will drive the colonization process and species distributions. A key assumption to developing specific predictions from the C-DIB model, however, is that variation in key traits is greater among species than within (McGill et al. 2006).

While all insular systems are subject to this general framework regarding colonization and extinction, the dynamics of these processes will vary depending on the nature and cause of environmental change (Box 1). Differences in island characteristics (and the environmental drivers of their cycling) will determine the duration and importance of extinction and colonization phases in shaping population and community-level processes. In the case of continental islands, it is expected that extinction will be the primary driver in species composition until a connection with the mainland is reestablished, allowing species to recolonize (Box 1a). In contrast, disturbance-isolated habitat patches should experience an initial wave of extinction followed by a period of gradual recolonization as the (semi-permeable) matrix recovers (Box 1c; Butaye et al. 2001).

Support from montane "sky islands"

Glacial–interglacial cycles provide exemplary "natural experiments" for evaluating predictions of the C-DIB model (Box 4) over large spatial extents and time scales. Warming climate and rising sea level since the Last Glacial Maximum continue to cause many mountaintop and continental shelf islands to shrink. It is not surprising that many such systems have undergone community disassembly via the extinction process (Patterson 1987, Wright and Reeves 1992, Lomolino 1993), for example, with their mammalian communities often losing the largest species and carnivores first (Brown 1971, Okie and Brown 2009). The "sky islands" of the Great Basin in western North America have been instrumental in both inspiring and evaluating biogeographic theory by highlighting historical factors that have influenced current communities (Brown 1971, Grayson and Livingston 1993, Rickart 2001, Rowe 2009). The extent of boreal forests in the Great Basin has cycled from expansive coverage, including both mountains and low-lying areas during glacial maxima, to isolated patches on mountaintops surrounded by a matrix of lowland desert scrub during interglacials. The forest habitats on these sky islands have been isolated from more contiguous boreal habitats in the Rocky Mountains since the shift out of the Last Glacial Maximum. However, the highest-elevation vegetation types (yellow pine, spruce, and fir) were probably not connected even during glacial times (Brown 1971). Supporting predictions of trait-mediated extinction, the smallest patches in these sky islands host mammalian communities characterized not only by lower richness but also: i) reduction in the range of body sizes present, ii) fewer species at high trophic levels, and iii) lack of specialists (Brown 1971, Grayson and Livingston 1993).

More recent evidence from the Great Basin sky islands has begun to reveal how the distribution of mammals across mountain top communities has been further shaped by trait-mediated colonization. Waltari and Guralnick (2009) used ecological niche models and reconstructions of past environments to quantify areas of suitable environment for montane species in the present; they then projected those models to the Last Glacial Maximum. Their finding that habitat connectivity varies among species and between time periods is consistent with previous observations that several species inhabiting nearby ranges of the Rocky Mountains – particularly those associated with yellow pine, spruce, and fir forests at the highest elevations – are not found in the sky islands despite suitable habitat area existing there today (Brown 1971). We argue that this provides preliminary support for the C-DIB model and shows the utility of using paleo-reconstructed niche modeling to further evaluate the hysteresis prediction of the C-DIB model (Box 4), where similar current island states can have different community composition due to previous environments. Moreover, the vastly different continental shelf islands of the Sunda Shelf in Southeast Asia show striking similarities in these patterns (Okie and Brown 2009, Burger et al. 2018), supporting predictions of the non-random extinction process of the model (Box 4). These systems show support for the C-DIB model that can be extended to other glacial–interglacial systems worldwide.

Future extensions: From candidate species pools to realized communities

While recognizing the inherent idiosyncrasies of many insular systems, we have presented a conceptual model that is deliberately simple with the aim of making general predictions using the fewest possible parameters (Marquet et al. 2014, Vellend 2016). The simple constraints proposed in the C-DIB model

Box 4. Hypotheses and predictions of the Constraint-based model of Dynamic Island Biogeography (C-DIB).

Hypothesis 1: Colonization probabilities vary among species according to the ability of individuals to cross the matrix and the species' affinity to the conditions in the matrix between mainland and island. The C-DIB model predicts that at the *Population-level*, a species will only be present on islands where at previous time periods the distance to the mainland was within individual dispersal range, or where suitability indicated connectivity to the 'mainland'. This emerges at the *Community-level* where, the C-DIB model predicts that insular communities will be overrepresented by species that had sufficiently small distances for individuals to traverse, or greater connectivity in the matrix during the previous cycle (e.g., Last Glacial Maximum in montane and continental shelf systems; Box 1).

Hypothesis 2: Once present on the island, extinction probabilities will vary among species according to the area required for sufficient resources to sustain a population. In general, larger species require greater areas and so would be absent from the smallest islands. The C-DIB model predicts that at the *Population-level*, species will only be present on islands whose area is at or above that predicted necessary to sustain a minimum viable population (Box 2). This leads to a *Community-level* prediction that each insular community will be underrepresented by species of the largest body sizes.

Hypothesis 3: Some islands may have suitable habitat that is sufficiently large in the present for a given species, yet the species is absent. This relates to the hysteresis prediction of the C-DIB model as it applies to the *Population-level*. Species are predicted only to be present on islands that have maintained suitable island size following a period of favorable island connectivity. This lends to *Community-level* prediction of asymmetric community compositions contingent on past environments (Box 3).

provide a powerful integrative framework to investigate the importance of trait-mediated colonization and extinction in island community dynamics and the possible hysteresis that may emerge. However, in many natural systems, additional processes will narrow or alter the predicted candidate species pool to the set of species actually occurring on the island at any particular point in time. In the following section, we highlight how some of these processes can be integrated to extend the C-DIB framework to particular real-world systems. Moreover, mathematical and simulation models should provide means to evaluate the influence of these additional factors and their importance for particular ecosystems and landscapes.

Time lags, extinction debts, and colonization credits

The predictions of the C-DIB model assume that populations are at a steady-state with the environment (and its history) at a given 'snapshot' in time. However, the processes of colonization and extinction can be complicated due to factors such as stochastic elements of patch occupancy, relative rates of environmental change, and life histories of the species involved (Hanski and Ovaskainen 2003, Colwell and Rangel 2010, Leibold and Chase 2018). In part because colonization and extinction are probabilistic processes, time becomes an important factor in the likelihood of either event occurring. For example, the longer island conditions remain below the minimum area necessary to sustain a population of a given species, the more likely the species will become extinct from the insular community. Such realities can result in time lags and discrepancies between theoretical predictions and empirical observations (Tilman et al. 1994, Jackson and Sax 2010, Kitzes and Harte 2015). For example, what is termed 'extinction debt' can occur when an island shrinks below a size required to sustain a population: some species may persist in the patch for a while but are doomed to extinction.

Similarly, 'colonization credits' can occur when island size has become sufficiently large and matrix conditions have become amenable, but species that could maintain their populations there have not yet colonized. These lags in predicted vs. realized island communities are likely to occur when the pace of environmental change is fast relative to the demographic rates of focal taxa. Existing theory and analytical approaches regarding the expansion and contraction of species distributions under dynamic environments as well as those concerning demographic processes linking population-level responses to environmental change (e.g., Mouquet and Loreau 2003, Leibold et al. 2004, Engler et al. 2009, Anderson 2013, Estrada et al. 2015, Vellend 2016, Leibold and Chase 2018) are ripe for integration with the C-DIB framework.

Biotic interactions

In the core C-DIB presented above, the effects of environmental constraints act independently on each species within the source pool irrespective of the composition of species occupying the given island community. In many insular systems, however, biotic interactions will undoubtedly play important roles in species establishment and persistence (e.g., Vannette and Fukami 2014). These include positive and negative effects such as exclusion, facilitation, trophic release, and priority effects (Cody and Diamond 1975, Fukami 2015). Interestingly, priority effects are themselves a form of hysteresis, and incorporating them into studies of extinction and colonization on dynamic islands has the potential to predict many complex outcomes.

Other types of biotic interaction may also result in unexpected consequences. For example, the extirpation of predators can cause cascading effects that lead to primary consumers exhausting their resources (e.g., Estes et al. 2011). Moreover, increasing connectivity may result in higher or lower species richness if some common species that occur across large spatial extents are also abundant in local communities (Mouquet and Loreau 2003, Leibold et al. 2004, Scheffer et al. 2006, Götzenberger et al. 2012, D'amen et al. 2017). Despite the difficulty in detecting and accounting for the effects of biotic interactions when estimating species distributions (e.g., Anderson 2017), recent work has made progress in elucidating the role of species traits in mediating direct and indirect interactions within populations and communities (Bolker et al. 2003, Werner and Peacor 2003, Lessard et al. 2016). Understanding which traits determine the relevance and intensity of both negative and positive interactions offers future research opportunities to advance the C-DIB framework.

Evolution on islands

Finally, the C-DIB model assumes that the effects of evolutionary processes on island community composition are minimal. Speciation has been highlighted as an important consideration for older, more distant oceanic islands (Heaney 2000, Whittaker et al. 2008). However, speciation *per se* may not be of large consequence when inferring the past or future distribution of species, even over timescales on the magnitude of glacial–interglacial cycles (Heaney 2000). In contrast, the power of evolutionary and cultural adaptations to shape the traits relevant for colonization and extinction does have the potential to affect predictions of island community composition (Leimu and Fischer 2008). For example, body size evolution on islands is well established (Lomolino 2005) and likely influences extinction outcomes. While trait evolution is not as likely to be an issue when considering islands that cycle on relatively short time scales (e.g. disturbance–succession islands), it becomes more important with increasing duration of environmental cycles (e.g., Steinbauer et al. 2012). Glacial cycles occur on time scales of 10,000–100,000 years (Bennett 1990, Roy et al. 1996), and the assumptions of niche conservatism for relevant traits over these scales (e.g., Waltari and Guralnick 2009) are more likely met for large organisms with slower generation times (e.g., large mammals and trees). However, complications due to such factors are likely to be present for small organisms with fast generation times relative to the timescale of the cycle. Considering rates of evolution in relation to timescales of environmental cycles and their influence on population and community dynamics is an important next step in advancing the C-DIB framework we have outlined here.

Coda

The C-DIB model builds on foundations laid by MacArthur and Wilson (1963, 1967) and many subsequent studies by integrating trait-based constraints on colonization and extinction in insular systems with environmental and spatial characteristics that cycle through time. Notably, it leads to novel predictions regarding hysteresis in island biogeography depending on the trajectory of environmental cycles. Such predictions provide a launching point to pursue empirical, mathematical, and simulation studies. In practice, the model has key implications for understanding the effects of habitat fragmentation on biodiversity as well as ongoing climatic shifts—two pervasive features of the Anthropocene. Recent availability of expansive biological and environmental datasets, the incorporation of functional traits into ecological theory (e.g., Enquist et al. 2015), and modeling tools such as those for ecological niche modeling (e.g., 'Wallace'; Kass et al. 2018) provide exciting opportunities to evaluate the C-DIB model across taxa in a variety of systems. Doing so should improve our understanding of the physical forces and biological constraints that act together on populations and communities that make up the spectacular diversity of life on Earth.

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