

Infinite graphs in systematic biology, with an application to the species problem

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Abstract

We argue that C. Darwin and more recently W. Hennig worked at times under the simplifying assumption of an eternal biosphere. So motivated, we explicitly consider the consequences which follow mathematically from this assumption, and the infinite graphs it leads to. This assumption admits certain clusters of organisms which have some ideal theoretical properties of species, shining some light onto the species problem. We prove a dualization of a law of T.A. Knight and C. Darwin, and sketch a decomposition result involving the internodons of D. Kornet, J. Metz and H. Schellinx. A further goal of this paper is to respond to B. Sturmfels' question, "Can biology lead to new theorems?"

Keywords: infinitary systematics, tree of life, Knight-Darwin law, species problem, internodons

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1 Introduction

Dress et al. (2010) recently renewed interest in the set of all organisms ever to have lived, endowed with a directed graph structure. We thought it a natural extension to consider the set V of organisms (or other living things) which have ever lived or which will ever live in the future. We found that this extension had already been made explicit in Kornet (1993) and Kornet et al. (1995), where the future is needed in order to distinguish between temporary and permanent splits in genealogical networks.

1.1 Darwin as Infinite Graph Theorist

With our future-oriented view of systematics in mind, we recalled that particularly relevant passage from C. Darwin’s *On the Origin of Species*:

The Knight-Darwin Law. (Darwin 1872) “...it is a general law of nature that no organic being self-fertilises itself for a perpetuity of generations; but that a cross with another individual is occasionally—perhaps at long intervals of time—indispensable.”

In (Francis Darwin 1898) we learn that the above principle is called the Knight-Darwin Law. But in a world where life goes extinct in finite time, this law is trivial: even if all reproduction in the entire world were asexual, the Knight-Darwin Law would still trivially hold for lack of an instance of “perpetual” (infinite) self-fertilisation to falsify it.

Thus not only is Darwin concerned with the distant future of life, he seems to admit the possibility of an infinite biosphere— the possibility that life will never go extinct— because if he explicitly thought this impossible, then there would be no point suggesting the above Law.

Based on a careful reading of surrounding passages, we believe the Knight-Darwin Law can be glossed in modern graph-theoretical language as follows (hereafter, G is the graph of all living organisms, past and future, an arc directed from u to v precisely if u is a parent of v):

The Knight-Darwin Law. (*Graph-theoretical version*)
The graph G does not contain an infinite directed path of vertices each of which has < 2 parents.

Darwin did know of apparent counterexamples (see Francis Darwin 1898), reducing the Knight-Darwin Law to a simplifying assumption; nevertheless, a simplifying assumption of remarkable graph-theoretical sophistication for its time. One might argue that infinite graphs were not well studied outside of cutting-edge research mathematics until (König 1936), many decades after Darwin’s work.

In a later section we will prove that if true, the Knight-Darwin Law logically implies a Dual Knight-Darwin Law.

1.2 Hennig as Infinite Graph Theorist

There is compelling reason to suspect the Figure 4 on p. 19 of W. Hennig’s (1966) book (see our Figure 1) implicitly depicts an infinite graph— joining Hennig with Darwin in infinite graph theory.

The figure in question illustrates a *cleavage* in a biological network. Hennig refers (in his caption) to “the process of species cleavage” (emph. mine), suggesting a dynamic continuation of the genealogical network (graph) splitting up. Thus (we believe) Hennig must intend the population to continue beyond what is shown (what is shown is too ephemeral to be a *process*). A finite continuation would have the same problem, thus suggesting an infinite intended extension. In the text accompanying the figure, Hennig speaks of species

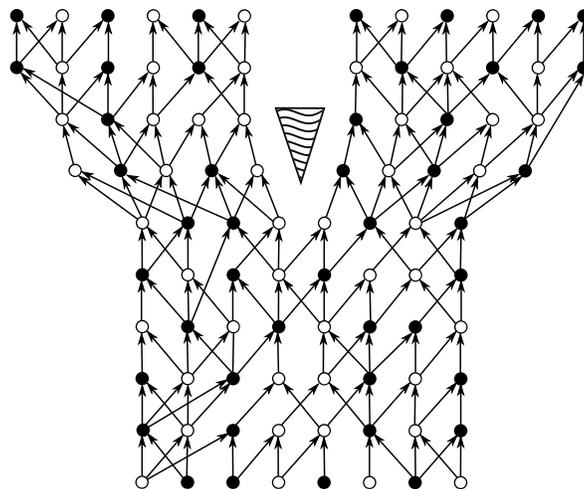


Figure 1: A reproduction of a graph in W. Hennig’s (1966) book (Hennig’s Figure 4, p. 19). If we understand correctly, the triangle denotes the permanency of the corresponding cleavage; this triangle would be superfluous if Hennig did not intend us to imagine the graph continuing beyond what is shown.

which “persist over long periods of time” but which are “not absolutely permanent”. Like the Knight-Darwin Law, there would be no reason to even mention absolute permanence if Hennig assumed a finite end to the biosphere.

Furthermore, Hennig seems to distinguish between one particular cleavage (indicated by a triangle) and smaller cleavages also present in the graph. Surely the distinction cannot be as arbitrary¹ as “branch size 26” versus “branch size 1”. Hennig discounted the minor cleavages because he meant us to imagine them as temporary— they would disappear if we just saw a little more of the graph. But any finite number of additional generations would still suffer minor cleavages² and the only way to eliminate them is to continue the graph infinitely far.

1.3 An Application to the Species Problem

The *species problem* is the problem of finding a proper definition for the intuitive concept of a biological species. Many species notions exist, each with its own pros and cons, and none have managed to reach universal acceptance.

By studying G with an explicit infinitude assumption, we have arrived at some cluster notions (described in Sections 3 and 4) which we have decided to call *infinitary genera* and *infinitary species*. These name choices will be justified below; *infinitary genus* is more or less an arbitrary name and could be replaced by *infinitary family* or *infinitary order* or *infinitary tree-of-life-node*; however, the name *infinitary species* is important.

We won’t pretend that our species notion is like any species notion used by everyday biologists; it would be useless in the field, and we would never dream of suggesting it as a replacement for the practical species notions. However, we hope our notion will apply to the species problem in three ways: by offering a solution to a species sorites paradox; by theoretically reconciling competing morphological and non-morphological approaches to species definition; and by telling us something about the structure of the far future extremities of the tree of life.

2 Some Further Justification for Infinitary Assumptions

“So profound is our ignorance, and so high our presumption, that we marvel when we hear of the extinction of an organic being; and as we do not see the cause, we invoke cataclysms to desolate the world, or invent laws on the duration of the forms of life!” —Charles Darwin (1872)

In assuming that infinitely many individuals will live, we are hardly the first scientists to approximate the finite by the infinite. The assumption is very similar to how physicists and chemists study symmetry groups of crystal patterns or tilings. We assume such patterns fill space to infinity, because otherwise it would be very unnatural, if possible at all, to sensibly talk about their translation symmetries— we wonder whether this might somewhat explain, by analogy, why species are so difficult to define.

2.1 Justification by Pursuit of New Mathematics

By assuming infinity we will obtain somewhat unique responses to Sturmfels’ (2005) question, “Can biology lead to new theorems?” If biology is to be “mathematics’ next physics, only better” (Cohen 2004) it must generously contribute to the combinatorial and infinitary branches of mathematics, as physics has done.

One way to distinguish mathematical theorems is on the strength of the set-theoretical assumptions which they require. To be sure, biology has already contributed much to mathematics, but the author is unaware of any theorems from biology which hinge on the *Axiom of Choice*; we will exhibit such a theorem in Section 4 (Theorem 3).

¹Baum & Shaw (1995, p. 294) and Velasco (2008, p. 868) point out the problem of *big* cleavages and *small* cleavages, and the resulting vagueness. This vagueness disappears under infinitary assumptions.

²Unless something unnatural occurred, for example, all the living specimens of each species joining to co-parent a single sterile child.

2.2 Reduced Dependence on Scale

There seems to be some disagreement on whether the systematist ought to focus on individual living organisms, or whether to zoom out and consider larger populations as atoms; see, for example, the back-and-forth between de Queiroz & Donoghue (1988) (pro-individual organisms) and Nixon & Wheeler (1990) (the opposite).

If the biosphere is finite, this scaling decision has a big effect on the shape of the biosphere. If one systematist takes organisms as atoms, and another takes some populations approximating species, the sizes of the resulting biospheres differ quite a bit.

On the other hand, if both systematists operate under the assumption of an infinite tree of life, their decisions do not effect the shape of the biosphere: viewed through either lens, the biosphere is infinite.

Note that this scaling decision can go both ways. Rather than considering individual organisms as the vertices of our graph, we could zoom *inward* and consider (say) individual X-chromosomes as vertices. In a finite world, this decision would massively blow up our graph G , but under infinitary assumptions, it makes no major difference.

2.3 A word to the most hardcore finitist

I hope my paper will be useful to you, too. In later sections there are results (e.g. Proposition 6) which are, I think, counter-intuitive enough that you might be able to get away with calling them paradoxes, and using them to advance the finitist argument by *reductio ad absurdum*, in the same way a critic of the Axiom of Choice might use the Banach-Tarski paradox. In other words, feel free to read the paper as a set of theorems specifically intended to *disprove* infinitary assumptions.

3 Infinitary Genera

In this and the next two sections, we will exhibit some interesting cluster notions which arise from the infinite biosphere assumption along with some additional assumptions which we consider less scandalous. The precise assumptions we make are as follows.

- (A1) We assume (like Dress et al. (2010)) there are only finitely many *roots*, that is, parentless individuals.
- (A2) We assume no individual is a parent of infinitely many children.
- (A3) We assume each vertex $v \in V$ has a *birthdate* $t(v) \in \mathbb{R}$, that $t(u) < t(v)$ whenever u is a parent of v , and that for every real x , $\{v \in V : t(v) < x\}$ (the set of individuals born before time x) is finite.
- (A4) We assume G is infinite, that is, infinitely many individuals will live.

We will define an infinitary genus to be an infinite set of individuals which is *closed under ancestry*, that is, which contains every ancestor of every member of itself. But it would be rash to make this definition without first motivating it. In mathematics, it is a sign of a notion's importance when it arises unexpectedly from seemingly-unrelated competing notions. We will arrive at our infinitary genus notion in precisely this way.

To be clear, we use the word *genus* arbitrarily where any of *family*, *order*, or *tree-of-life-node* would work just as well. Mathematical language is great for speaking about things which are maximal (e.g. the entire biosphere) and things which are minimal (e.g. infinitary species, as we'll see in the next section) but not at distinguishing between different intermediate levels (e.g. genera vs. families).

With the above paragraphs in mind, let us make the following attempt at defining a group of individuals. We will define what we call a *birthdate genus*. Our hope is that this is particularly obvious, something the reader could easily invent on their own. We will then prove it to be equivalent to our desired infinitary genus notion, in sight of Assumptions A1–A4. Thus the following definition will not itself feature prominently in the rest of the paper, its purpose is to motivate a definition to come after.

Definition 1. By a *birthdate genus* I mean a set S of individuals such that there is some time t such that every member of S has birthdate $\geq t$ and every external ancestor (that is, every individual outside S but with a descendant in S) has birthdate $< t$.

As a clustering notion, this is a weakened version of the much stronger notion which Dress et al. call the *Apresjan cluster*, following Steel (2007). It captures the intuition that a node in the Tree of Life must have evolved into existence at some particular time, and thus, all its members are at least that young, while every external ancestor is strictly older.

Convention 2. If X and Y are infinite sets, we say X is *almost equal to* Y (and write $X \approx Y$) if their symmetric difference $(X - Y) \cup (Y - X)$ is finite.

The whole reason to define birthdate genera was to allow the following motivating result:

Proposition 1. If S is an infinite set of individuals, then the following two conditions are equivalent:

1. S is almost a birthdate genus.
2. S is almost its own ancestral closure.

Proof. Let \bar{S} be the ancestral closure of S .

(1 \Rightarrow 2) Assume S is almost a birthdate genus. Thus, there is a birthdate genus S' such that $S \approx S'$. There is some time t such that all members of S' are born at time $\geq t$ and all external ancestors of S' are born at time $< t$.

Now, we claim that $\bar{S} - S$ is finite. Suppose $u \in \bar{S} - S$. Since $u \in \bar{S}$, u is an ancestor of an individual $v \in S$. There are three cases:

- Case 1: $u \in S' - S$. Since $S' - S$ is finite, this can only occur for finitely many u .
- Case 2: $u \notin S' - S$ and $v \in S'$. Then u is an external ancestor of S' , so is born before time t . By Assumption A3, this can only occur for finitely many u .
- Case 3: $u \notin S' - S$ and $v \notin S'$. Since $v \in S$, $v \in S - S'$. Since $S - S'$ is finite, there are only finitely many possibilities for v , and Assumption A3 implies that those finitely many possibilities only have finitely many ancestors, so again, Case 3 can only occur for finitely many u .

This shows $\bar{S} - S$ is finite. Since $S - \bar{S} = \emptyset$ is also finite, $S \approx \bar{S}$ as desired.

(2 \Rightarrow 1) Conversely, assume $S \approx \bar{S}$. Thus, there are only finitely many external ancestors of S , call them S_1 . Of these finitely many individuals, let t be the latest birthdate which occurs. By Assumption A3, only finitely many individuals were ever born as of time t , call them S_0 . We claim $S - S_0$ is a birthdate genus. Certainly any member of $S - S_0$ is born after time t , by definition of S_0 . Now suppose $v \notin S - S_0$ has a descendant in $S - S_0$. It could be $v \in S_0$, in which case v 's birth date is no later than t , by definition of S_0 . Otherwise, v must be outside of S , and thus, having a descendant in S , v is in S_1 , so that (by choice of t), again v is born no later than t . \square

If we ignore finite sets as being insignificant, and treat infinite birthdate genera as being identical to sets which are *almost* infinite birthdate genera, we arrive (via Proposition 1) at a much simpler definition, and one which is easier to work with, at the price of an error which is infinitesimal.

Definition 3. An *infinitary genus* is an infinite, ancestrally closed set of individuals.

Right away we would like to demonstrate how closely interwoven Definition 3 is with the point-set topology of cladistics: further evidence of the legitimacy of the definition and its worthiness of study.

Proposition 2. An infinite set S is an infinitary genus if and only if it is a closed set in the topology on V where clades are the basic open sets (by a *clade* of course we mean an individual and its descendants).

Proof. In other words, we must show that for infinite S , S is an infinitary genus if and only if its complement S^c is a union of clades.

(\Rightarrow) Assume S is an infinitary genus. Let $v \in S^c$. Since S is ancestrally closed, v cannot be an ancestor of any element of S . Thus, the clade C_v , consisting of v and all its descendants, is disjoint from S . Therefore S^c is the union

$$S^c = \bigcup_{v \in S^c} C_v$$

of clades.

(\Leftarrow) Assume S^c is a union of clades and let $v \in S$ have an ancestor u ; we must show $u \in S$. If u were not in S , u would be in S^c , hence in some clade entirely contained in S^c . But v would be in that clade, forcing $v \in S^c$, a contradiction. \square

4 Infinitary Species

The motivation for our species notion is the conviction that species should be the smallest taxa— below genera, families, orders and so on. Thus, we will define an infinitary species to be an infinitary genus in which no proper subset is an infinitary genus.

But why does such an obvious-seeming approach work for us when it has not worked for the finitist? If a set of organisms constitutes a species, then presumably it would still constitute a species if one specimen were eliminated. According to our minimalist approach, if we could throw that specimen out of the species and still have a species, then we must do so. In a finite world, this repeated act of discarding specimens would render the species empty. This is an instance of the sorites paradox, or paradox of the heap (Hyde 2011). However, there is a way out of the trap: if we require our species to be infinite and ancestrally closed, the premise that we can always discard one specimen and retain a species gains a caveat: we cannot discard the specimen if it has so many descendants that doing so would render the species finite. We shall see that this causes the sorites paradox to vanish.

Definition 4. An *infinitary species* (or more simply an *inspecies*) is an infinitary genus in which no strictly smaller infinitary genus is a subset.

A priori, there might be no inspecies— either because of the sorites paradox, or because infinitary genera can be refined further and further with no end. The main technical theorem of this paper is:

Theorem 3. Given assumptions A1–A4, there is at least one inspecies.

The proof will use the Axiom of Choice, in its Zorn’s Lemma (Zorn 1935, Gowers 2008) form³. We will briefly review Zorn’s Lemma before proving the theorem (we state the lemma in a form most suitable for the use to which we will apply it). A reader willing to take our word for it can safely skip the proof, but bear in mind that if any one of A1, A2, A3, or A4 were denied, the other three would not imply the theorem.

Recall that a binary relation \supseteq on a set \mathcal{X} is a *partial order* if it is reflexive, transitive, and anti-symmetric (anti-symmetry means that if $X \supseteq Y$ and $Y \supseteq X$ then $X = Y$). A family $(Z_i)_{i \in I}$ of elements of \mathcal{X} , indexed by a linear order I , is a \supseteq -*chain* if

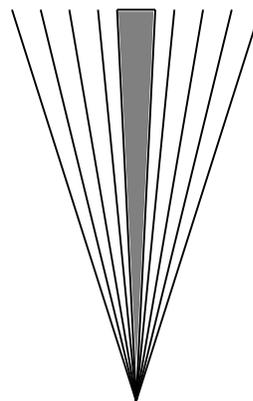


Figure 2: A species (shaded) nested within a larger genus, within a larger order, within a larger family, and so on.

³By A3, the biosphere is countable; it can be shown that only the *countable* axiom of choice is needed to guarantee existence of inspecies.

$Z_i \supseteq Z_j$ whenever $i \leq j$. A *bound* for this chain is an element $Z \in \mathcal{X}$ such that $Z_i \supseteq Z$ for every $i \in I$. An element $X \in \mathcal{X}$ is *extremal* if the only $Y \in \mathcal{X}$ such that $X \supseteq Y$ is $Y = X$ itself.

Theorem 4. (*Zorn's Lemma*) Let \supseteq be a partial order on a nonempty set \mathcal{X} . Suppose that every nonempty \supseteq -chain has a bound. Then \mathcal{X} has an extremal element.

Armed with this mathematical logical sledgehammer, we can prove Theorem 3.

Proof of Theorem 3. We may assume the following (*): that every non-root individual is a descendant of every root. This is safe to assume because if it is untrue, we can (thanks to A1) add an imaginary “super root” to our graph and declare it to be the lone parent of all actual roots.

Let \mathcal{X} be the set of all infinitary genera. Notice $\mathcal{X} \neq \emptyset$ since it contains V itself: the set of *all* individuals is an infinitary genus by Assumption A4. Notice that the superset relation \supseteq partially orders \mathcal{X} , and an infinitary genus $X \in \mathcal{X}$ is an inspecies precisely if it is extremal with respect to \supseteq . Therefore, by Zorn's Lemma, it is sufficient to let $(Z_i)_{i \in I}$ be an arbitrary nonempty \supseteq -chain from \mathcal{X} and show it has a bound in \mathcal{X} . We will show that $Z = \bigcap_{i \in I} Z_i$ is such a bound. Obviously for every $j \in I$, $Z_j \supseteq \bigcap_{i \in I} Z_i$, so all that remains is to show $\bigcap_{i \in I} Z_i$ is in \mathcal{X} (i.e., that it is an infinitary genus).

First the easy part: we show that $\bigcap_{i \in I} Z_i$ is ancestrally closed. Let $v \in \bigcap_{i \in I} Z_i$ and let u be an ancestor of v . For every $i \in I$, we have $v \in Z_i$, and Z_i is ancestrally closed, so $u \in Z_i$; by arbitrariness of i , this shows $u \in \bigcap_{i \in I} Z_i$, establishing ancestral closure of Z .

The difficult part is to show that Z is infinite. Assume, for sake of contradiction, that Z is finite.

Let q_1, \dots, q_m be those individuals who have a parent in Z but who are not in Z themselves: there are finitely many of these by Assumption A2. For any $1 \leq k \leq m$, the fact that $q_k \notin Z = \bigcap_{i \in I} Z_i$ means there is some $i_k \in I$ such that $q_k \notin Z_{i_k}$, and thus (since $(Z_i)_{i \in I}$ is a chain) more strongly $q_k \notin Z_i$ whenever $i \geq i_k$. Therefore, letting $i = \max\{i_1, \dots, i_m\}$, we have: $q_1 \notin Z_i, q_2 \notin Z_i, \dots, q_m \notin Z_i$.

Now, Z_i is infinite since it's an infinitary genus. Thus $Z_i - Z$ is infinite since Z is finite. In particular, $Z_i - Z$ is nonempty. Thus, we can pick an individual $r \in Z_i - Z$ with shortest possible reverse-path to a root (every individual has a reverse-path to a root by Assumption A3). By (*), Z contains all roots, so r is not itself a root, and that shortest path is not the empty path. So r has a parent on that minimal-length path. This parent *must* be in Z , because otherwise, we would have chosen the parent instead of r (the parent has a shorter path to a root).

I've shown that r has a parent in Z , but r itself was chosen outside Z . By definition this means r is one of the q_1, \dots, q_m . This is nonsense, because $r \in Z_i$ and all of the q_1, \dots, q_m are absent from Z_i .

By contradiction, Z is infinite, and so (being ancestrally closed) it is an infinitary genus. I've shown that an arbitrary nonempty chain has a bound; by Zorn's Lemma, \mathcal{X} has an extremal element, i.e., there is an inspecies. \square

5 Results

The key to the structural properties of inspecies is the following result, remarkable for being so powerful while having such a simple proof.

Proposition 5. Suppose C is an inspecies and $S \subseteq C$ is any infinite subset. Then every individual in C has a descendant in S .

Proof. Let C' be the set of ancestors of individuals in S . Then C' is clearly ancestrally closed; since S is infinite, Assumption A2 implies C' is infinite; altogether, C' is an infinitary genus. And $C' \subseteq C$ since C is ancestrally closed, so $C' = C$ by minimality. \square

This has remarkable consequences for individuals within inspecies. Take any property P , which may hold of some individuals and not hold of other individuals. Within an inspecies, every individual has a descendant with property P , or every individual has a descendant without property P (or both). For instance, in an inspecies everybody has a vertebrate descendant, or everybody has an invertebrate descendant. If there is a fixed universal upper bound on the number of hairs an individual can have on their body, then for any inspecies, there is some number n such that everybody in the inspecies has a descendant with exactly n hairs on their body. If we let Bertrand Russell choose the property P , he would no doubt choose the property “not a descendant of Bertrand Russell” and thereby lead us to:

Proposition 6. In an inspecies, every individual is an ancestor of almost every individual.

Proof. Let u be a member of an inspecies and let S be the set of members of that inspecies who are not descended from u . If S were infinite, then by Proposition 5, u would have a descendant in S , which is absurd. So S is finite, meaning almost every member of the inspecies descends from u . \square

With Proposition 6 in our arsenal we can productively compare the inspecies with the *tight cluster* notion of Dress et al. If C is an inspecies and we let $D(\supset_{\approx} C)$ consist of all individuals in V whose descendants include *almost* all of C , then Proposition 6 implies $D(\supset_{\approx} C) = C$. Therefore, every inspecies is a kind of one-sided version of a tight cluster (it is one-sided because the clusters of Dress et al. (2010) are designed to be closed descendantially (at least when unborn future individuals are ignored) and ours are not). A similar observation goes for Baum’s (2009) concept of *organismic exclusivity* (as described by Dress et al.)

The next proposition will theoretically reconcile morphological and non-morphological approaches to the species problem.

Proposition 7. (*Morphological Trichotomy*) Let C be an inspecies and let P be a property of individuals. Exactly one of the following is true:

1. P holds of almost every member of C ,
2. P fails of almost every member of C , or
3. every member of C has both a descendant satisfying P and a descendant failing P .

Proof. Immediate by Proposition 5: if neither (1) nor (2) holds, then both the P -conformists and the P -rebels are infinite in number. \square

For example, in an inspecies of birds, a property of type 1 might be “has feathers”, a property of type 2 might be “has gills”, and a property of type 3 might be “is male”, or even “hatched between Monday and Thursday”.

In our opinion, Proposition 7 theoretically reconciles morphological species notions (recognizable, ecological, phylogenetic, and so on) with non-morphological species concepts. Inspecies are defined solely based on ancestral relations with reckless disregard for any other considerations— and yet, Morphological Trichotomy (Proposition 7) rigorously shows that morphological aspects of species are hard to avoid.

If we have understood him correctly, de Queiroz (2007) would say that the uniformities suggested by Proposition 7 are what he calls *former secondary species criteria*, which “can be used to define subcategories of the species category— that is, to recognize different classes of species” and which, therefore, we submit as evidence verifying we are justified in referring to infinitary species as a species notion.

Proposition 8. If two inspecies have infinite intersection, they are equal. That is, distinct inspecies have almost no members in common.

Proof. Let C_1 and C_2 be two inspecies with $|C_1 \cap C_2| = \infty$. By symmetry it’s enough to show $C_1 \subseteq C_2$. Let v be an individual in C_1 . By Proposition 5, v has a descendant in $C_1 \cap C_2$, hence in C_2 . Since C_2 is ancestrally closed, $v \in C_2$. \square

Sadly, our infinitary genus notion does not have the coveted *nesting property* described by Dress et al. On the other hand, Proposition 8 shows that (ignoring finite sets) inspecies have that property *too* strongly! By this we mean that if we copy the techniques in Dress et al. (2010) to turn a nested cluster notion into a forest notion, we get a degenerate forest with all vertices isolated and no arcs at all. This hints that, where the Tree of Life is concerned, inspecies may be the “leaves at infinity,” while the clusters of Dress et al. (2010) or the composite species of Kornet and McAllister (2005) may be the actual nodes.

As promised in the introduction, we will now prove that the Knight-Darwin Law implies a Dual Knight-Darwin Law (see Figure 3).

Theorem 9. Assume the Knight-Darwin Law: that G has no infinite path of vertices each with < 2 parents. Assume also that A1–A4 hold. Then the following facts are implied:

1. (*The Dual Knight-Darwin Law*) No inspecies has an infinite path of vertices each with < 2 children.
2. There are infinitely many individuals each of whom has multiple children.
3. Within an inspecies, every individual has a pair of descendants that breed together.

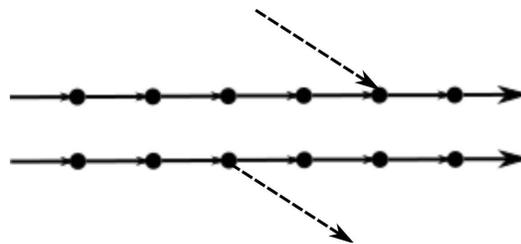


Figure 3: The Knight-Darwin Law (top) and the Dual Knight-Darwin Law (bottom).

Proof. (1) Let C be an inspecies, and let v_1, v_2, \dots be any infinite path in C . We must show some v_i has ≥ 2 children. For sake of contradiction, assume not. By the Knight-Darwin Law, there is some v_{i_1} with ≥ 2 parents. And then, by the Knight-Darwin Law applied to $v_{i_1+1}, v_{i_1+2}, \dots$, there is some v_{i_2} ($i_2 > i_1$) with ≥ 2 parents. This process continues forever: there are $i_1 < i_2 < i_3 < \dots$ such that each v_{i_j} has ≥ 2 parents. For each $j > 1$, let p_j be a parent of v_{i_j} different than $v_{i_{j-1}}$. All these new parents are in C by ancestral closure, and by Assumption A2, there are infinitely many of these new parents. By Proposition 5, one of the p_j is descended from v_1 . So v_{i_j} has at least two distinct parents, $v_{i_{j-1}}$ and p_j , both of whom are descended from v_1 (or possibly one of them could equal v_1). This implies (by acyclicity) that if we look at the path v_1, \dots, v_{i_j} , there must have been a fork somewhere, in order for p_j to be born and breed with $v_{i_{j-1}}$. This contradicts the assumption that none of the v_i 's have ≥ 2 children.

(2) Immediate from (1) along with Theorem 3.

(3) Let v be an individual in an inspecies C . By Proposition 6, there are only finitely many individuals in C not descended from v , and by Assumption A2, these finitely many non- v -descendants have only finitely many children. Thus, there must be some individual in C descended from v , both of whose parents are also descended from v . Those two parents are therefore a pair of descendants of v which breed together, as desired. \square

5.1 A Response to Sturmfels

B. Sturmfels asked (2005): “Can biology lead to new theorems?” We have self-imposed upon ourselves three *criteria* that we feel obliged to meet in order to satisfy ourselves in responding. In our opinion, in order for a mathematical biology paper to “Lead to new theorems,” it should:

- (T1) Include simple and interesting theorems about some new type of system motivated by biology.
- (T2) Demonstrate breadth, by using the new system to give original new proofs of some already known results (or open problems).
- (T3) Demonstrate nontriviality, by stating a nontrivial open problem which is not too contrived.

If we have erred in these criteria, we have attempted to err on the side of stringency. T3 could of course be replaced by the inclusion of a theorem with an interesting and difficult proof (e.g. a *non*-open problem).

For T1, we consider Theorem 3 and Propositions 5, 6, 7, and 8 sufficient. We have given some interesting theorems about new systems motivated by biology.

For T2, we consider Theorem 9 partially satisfactory. We consider it common knowledge that a genealogical human family tree must necessarily either keep branching (in the sense of multiple children being born of a parent) or keep bringing in new roots via marriage, or both, and if it stops doing so, successive generations will dwindle in size until extinction. Theorem 9 (part 2) formalizes this, and (part 1) (along with Theorem 3) generalizes it. Likewise, Theorem 9 (part 3) formalizes, strengthens, and reproves a certain notion that inbreeding is unavoidable. The original notion is that if we assume no inbreeding, then going back (say) 50 generations we should expect a human population of at least $2^{50} \approx 10^{15}$ by counting nothing but the distinct great⁴⁸-grandparents of this author. To satisfy T2 further, we have used infinite graphs in

systematic biology to give an alternate proof (in (Alexander, preprint)) of a result from (Johnston 2010) about Conway’s Life-like games.

For T3, we state the following open problem.

Open Problem. If $s = (s_0, s_1, \dots)$ is an infinite sequence from the alphabet $\{M, F\}$, say that s is *biologically unavoidable* if in every possible gendered population conforming to A1–A4 (*gendered* here meaning that every non-root has a male parent and a female parent), there is a sequence of organisms, each a parent of the next, whose genders match s (the sequence does not need to begin with a root). What are the biologically unavoidable sequences?

A priori, it could be that every sequence is biologically unavoidable. But in (Alexander, preprint) we show a counterexample (see Figure 4). It could also be, a priori, that *no* sequence is biologically unavoidable, but in the same paper, we show that every eventually-periodic sequence is unavoidable. It remains an open question even whether there is a single unavoidable sequence not eventually periodic.

Note, the result about every eventually periodic sequence being unavoidable could not be true if the sequences of organisms were required to start at a root, as the following example shows. According to J. Diamond (1997), “In an extreme scenario the first settlers [of Australia] are pictured as . . . a single pregnant young woman carrying a male fetus”. Define the set of *Aboriginals* to consist of that Mother, her Child, her Child’s Father, and all the joint descendants of the Mother and Child. Thus, the *roots* are exactly the Mother and the Father. Even if we assume the Aboriginals satisfy the hypotheses of the Problem, there can be no sequence starting at a root and having genders M, F, M, F, \dots , for the simple reason that there is only one male root and he has no female Aboriginal child.

The theorems in this section are certainly not exhaustive. We have opted to limit ourselves to theorems of particular interest in systematic biology. We hope they are adequate to establish infinitary genera and species as at least a potential candidate for a two-way bridge between biology and the more abstract and theoretical side of mathematics.

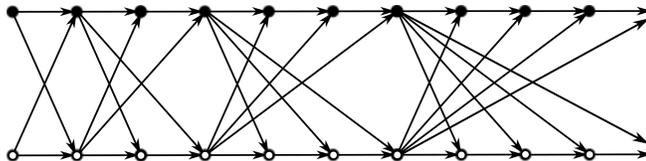


Figure 4: A hypothetical population (modified from an example of T. J. Carlson) in which not every gender sequence is realized. Solid vertices represent males and open vertices represent females. One particular sequence absent in this population is $M^2FM^5F \dots M^{3n-1}F \dots$.

6 Infinitary Species and Internodons

There are noteworthy similarities between infinitary species and the internodal species concepts of⁴ Kornet (1993), Kornet, Metz, and Schellinx (1995), and Kornet and McAllister (2005) (we shall focus on the 1995 paper, as it is mathematically the most straightforward).

Informally, internodons are⁵ the largest clusters subject to the constraint that *permanent splits* in the genealogical network give rise to new internodons. Thus, if (as in Figure 1) a branch in G splits permanently into two smaller branches, near the splitting point there are three internodons: one for the branch pre-split, and two for each smaller branch.

The primary similarity between internodons and inspecies is the dependence on the *future* (to establish a split’s permanence may require infinitely futuristic knowledge). Both are defined purely from G (and birthdates), *sans* morphology. Both respect permanent splits (individuals on opposite sides thereof can share neither an internodon nor an inspecies). And both notions arose from attempts to bridge math and biology: Kornet et al. attempted to derive new biology from math, and this author attempted to derive new math from biology.

⁴This work reflects a stepwise formalization of Hennig’s internodal species: unavoidability of the implied permanency of cleavages (Kornet, 1993), formal implementation (Kornet et al. 1995); lowering species’ status, because of implied short lifespans, to building blocks (internodons) (Kornet et al. 1995); remedial grouping by secondary morphological criteria into composite species (Kornet & McAllister, 2005). The entire project was first informally printed as a PhD thesis (*Reconstructing Species; Demarcations in Genealogical Networks*, 1993, Leiden University).

⁵To quote Kornet et al. (1995), internodons are “parts of a genealogical network of individual organisms between two successive permanent splits or between a permanent split and an extinction event.”

Our attempt to *contrast* inspecies and internodons leads to another application of infinite graphs to the species problem, the idea of benchmark populations.

6.1 Benchmark Populations

As the species problem is difficult, one strategy might be to try to solve tiny sub-problems. A *benchmark population* is a hypothetical population, together with a question which would be trivial in sight of a species problem solution. One such question might be, “does this population include members of multiple species, or just one?” If we solve the species problem, such a question should be straightforward. Til then, these questions are species sub-problems, which we might hope to answer before answering the full species problem.

Interesting benchmark populations will most likely be infinite. As the following example will show, a good benchmark population is one which exhibits some “edge case” pathology specifically meant to push species notions to their limits.

Our attempt to contrast inspecies and internodons led us to a particular benchmark population which we call the *one-third variant population*⁶ (see Figure 5). This population consists of infinitely many generations, each with one *male*, one *female*, and one *variant*. Each generation’s male and female produce the next generation’s male and female, and each generation’s female and variant produce the next generation’s variant. The question is: are the variants in the same species as the non-variants?

Any well-defined species notion (depending only on graph-theoretical considerations) should either answer the above question, explain why the question is ill-posed, or else use assumptions about reality which rule out the $\frac{1}{3}$ -variant population.

Internodal species notions say that variants are in the same species as non-variants (there are no splits in sight). Infinitary species say that the variants are *not* the same species: in fact the variants are not in any inspecies at all (lest the directed path of variants would violate the Dual Knight-Darwin Law (Theorem 9 part 1)).

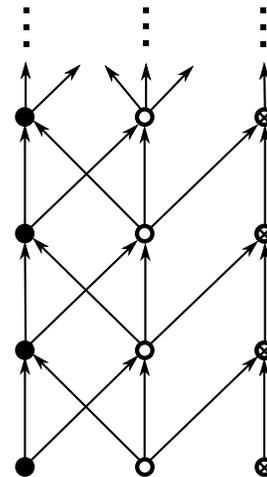


Figure 5: The $\frac{1}{3}$ variant population.

6.2 Infinitary Species (Type II)

Kornet et al. (1995) suggested that internodons are species building blocks (a suggestion bearing fruit in Kornet & McAllister (2005)). This raises one’s hopes that perhaps infinitary species are unions of internodons. The $\frac{1}{3}$ -variant population dashes those hopes.

This motivates a species notion using the same principles as inspecies but admitting decomposition into internodons. With the $\frac{1}{3}$ -variant population in mind, what must be found is a sense in which, e.g., a variant is an “ancestor” of later non-variants.

Note that in general u is an ancestor of v if and only if u is older than v and G has a *directed* path from u to v avoiding vertices older than u . So call u an *undirected-ancestor* (or simply an *undirancestor*)⁷ of v if u is older than v and G has an *undirected* path from u to v avoiding vertices older than u . Figure 6 shows a small population (left) and the corresponding undirancestral relations (middle). The latter clause— that G contains such an undirected path— is written $u(\mathbf{PC}_{\geq u})v$ in Kornet et al. (1995), a notation we too shall adopt. This makes variants undirancestors of future non-variants in the $\frac{1}{3}$ -variant population. Say a set of individuals is *undirancestrally closed* if it contains all its own undirancestors.

⁶As candidates one may think of organisms with complex haploid/diploid life cycles such as social animals (ants, bees, termites, weevils) or the creative algae, fungi, mosses. But simpler still would be a genuine sexual network with an additional *variant male type* with a y' chromosome. Say, this variant male’s sperm cells carrying the y' chromosome always outcompete its own sperm cells carrying the x chromosome. Then, per generation we have one (non-variant) *genuine xy male* (generating x and y sperm cells), one (non-variant) *genuine xx female* (generating x egg cells only), and one *variant xy' male* (generating y' sperm cells that always outcompete its x sperm cells). In this way a *variant* can only co-parent (with the *genuine female*) an xy' variant son.

⁷Thus, the undirascendants of u are precisely the members of the *gross dynasty* of u (minus u and its same-exact-age peers), in the language of Kornet et al. (1995).

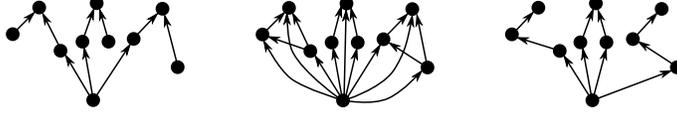


Figure 6: Left: A small population and its parental relations (birthdates indicated by vertical height). Middle: Its undirancestral relations. Right: Its undirparental relations.

Say u is an *undirected-parent* (or simply *undirparent*) of v if u is an undirancestor of v and there is no w such that u is an undirancestor of w and w is an undirancestor of v (this is a general recipe for reverse-engineering parenthood notions from ancestorhood notions). Figure 6 shows a small population (left) and its undirparent relations (right).

We'd like to apply our infinitary species machinery to undirparenthood. But first we must ensure we have not corrupted any of Assumptions A1–A4.

Lemma 10. Let G' be the graph whose vertices are the organisms of G , and in which an arc is directed from u to v if and only if u is an undirparent of v ; endow G' with the same birthdates as G . Given that G satisfies A1–A4, so does G' .

Note that in the graph G' of the lemma, for any vertices $u, v \in G$, u is an undirparent (resp. undirancestor) of v in G iff u is a parent (resp. ancestor) of v in G' .

Proof of Lemma 10. G' Satisfies A1. First we claim (*) that any vertex (say v) with a parent (say u) must have an undirparent. If u is an undirparent of v , this is trivial. Otherwise, since u is clearly an undirancestor of v , there is some w blocking u from being an undirparent of v . If w is an undirparent of v , we're done; if not, there is some w' blocking w from being an undirparent of v ... this process must terminate, because (by A3 in G) there are only finitely many individuals born before v . This proves (*). The contrapositive of (*) says: any individual with no undirparent must have no parent. There are only finitely many such individuals, since G satisfies A1.

G' satisfies A2. Let $u \in V$, we must show u has only finitely many undirchildren. Assume, for sake of contradiction, u has infinitely many undirchildren. By A3, only finitely many vertices share u 's birthdate, and by A2 these have finitely many children, so, by A3 again, u has an underchild v younger than all children of all vertices with u 's birthdate. Since u is an undirancestor of v , there is an undirected path $u = u_0, \dots, u_n = v$ avoiding vertices born before u . Let $j < n$ be maximal such that $t(u_j) = t(u)$. We chose v younger than all children of u_j , so $n > j + 1$. Thus it makes sense to pick $j < i < n$ such that u_i is as old as possible among all such choices for i . Since u_0, \dots, u_n witnesses $u(\mathbf{PC}_{\geq u})v$, it follows that u_0, \dots, u_i witnesses $u(\mathbf{PC}_{\geq u})u_i$. By maximality of j , $t(u_i) > t(u)$, so this shows u is an undirancestor of u_i . Since u_i was chosen as old as possible among $v_{j+1}, \dots, v_{n-1}, u_i, \dots, u_{n-1}$ avoids vertices born before u_i . And $u_n = v$ is younger than u_i , because $t(u_i) \leq t(u_{j+1})$ (by choice of i) and $t(u_{j+1}) < t(v)$ (by choice of v , since u_{j+1} is a child of u_j , which has u 's birthdate). Thus u_i, \dots, u_n witnesses $u_i(\mathbf{PC}_{\geq u_i})v$, and since $t(u_i) < t(v)$ this shows u_i is an undirancestor of v . Letting $w = u_i$, this violates the definition of u being an undirparent of v , a contradiction as desired.

G' satisfies A3. If u is an undirparent of v , then in particular u is an undirancestor of v , so by definition $t(u) < t(v)$. The other part of A3 (the finiteness of $\{v \in V : t(v) < x\}$) is trivial since G' has the same birthdates as G .

G' satisfies A4. G is infinite (by A4), and G' has the same vertices, so G' is infinite. \square

One very special case is if we assume no two organisms ever share a birthdate.

Proposition 11. Let G' be as in Lemma 10. If no two vertices share the exact same birthdate, then G' is a forest.

Proof. Assume no vertices share the same birthdate. To show G' is a forest, it suffices to show G' contains no cycles. By A3, existence of a cycle in G' implies some organism u has ≥ 2 distinct undirparents v_1, v_2 . By hypothesis, $t(v_1) \neq t(v_2)$, we may assume $t(v_1) < t(v_2)$. It follows v_1 is an undirancestor of v_2 (we have $v_1(\mathbf{PC}_{\geq v_1})v_2$ via u); letting $w = v_2$ violates the definition of v_1 being an undirparent of u . \square

In Figure 7, we induce unique birthdates in the network from Hennig’s Figure 4 by slightly tilting it; thin edges are Hennig’s original parental relations, thick edges are undirparental relations (which make a tree, with precisely one splitting point exactly where internodal speciation occurs). Note we assume the minor cleavages late in the network are temporary (i.e., that the network continues beyond what is shown, and minor branches rejoined later).

By an *infinitary species (type II)* for G , I mean an infiny species for the graph G' of Lemma 10. In other words, an infiny species (type II) is an infinite set of individuals closed under undirancestry and which cannot possibly be shrunk while preserving these properties. With A1–A4, an inspecies (type II) exists by Lemma 10 and Theorem 3. All the results from Section 5 carry over to inspecies (type II), with the prefix “undir” attached appropriately. For example, Proposition 6 says that within an inspecies (type II), everyone is an undirancestor of almost everyone. In case no organisms share the exact same birthdate, infiny species (type II) are simply the infinite branches in the forest G' .

The following theorem relates internodon theory and inspecies. For the sake of clarity and length, this theorem is stated with extreme simplifying assumptions; in future work we will generalize it to make it more applicable to the real world.

Theorem 12. Assume that no two individuals are born simultaneously, and that every individual has at least one descendant which has more than one parent. Then every inspecies (type II) is a union of internodons.

In Kornet et al. (1995), the property (above) that an individual has at least one descendant with multiple parents is called the **SD**-property (for Sexual Descendant).

The proof of the theorem is given in Appendix A. In future work when we strengthen this theorem, the strengthened version will involve the Knight-Darwin Law, tying together three central themes of this paper.

7 Discussion

What began with an attempt to generalize a graph of Dress et al. by considering future organisms as well as present and past, led us to consider some existing usages of the future biosphere in systematic biology. We noticed that at least one of these (the Knight-Darwin Law) and probably more (Hennig’s internodal species concept) hinge upon infiny assumptions, leading us to consider *infinite graphs in systematic biology*. Laboring under the (simplifying) assumption that the biosphere will be infinite, we found some natural cluster notions with some idealized properties of species.

Defined entirely by ancestral relations, infiny species share an *intrinsic* quality with other cladistical or non-morphological notions. And yet, Proposition 7 shows despite this, we still enjoy certain *recognizable* qualities associated with morphological species notions. We consider this an application to the species problem because it demonstrates that these seemingly unreconcilable approaches can actually meet when viewed at sufficient scale. Methods of Dress et al. suggest (in light of Proposition 8) that infiny species play the role of leaves at the distant future extremities of the tree of life.

The main flaws of infiny genera and species are as follows. First, they are completely unobservable: to establish even one organism’s membership in one particular infiny genus, it is necessary to have knowledge of the infinitely distant future. Second, not all organisms are guaranteed membership in any infiny

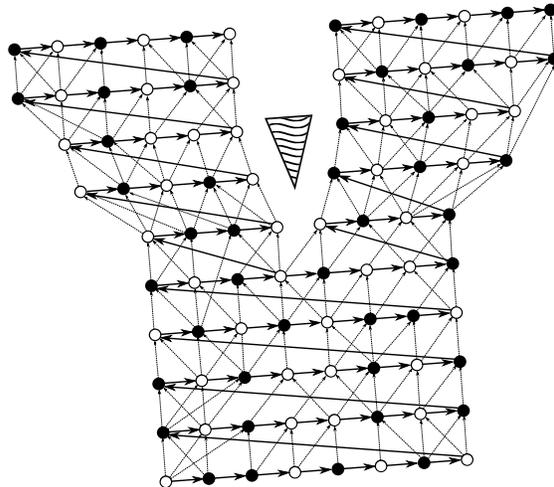


Figure 7: Undirparental relations in a copy of Hennig’s Figure 4 population, tilted to induce unique birthdates. We assume the population continues beyond what is shown, in particular that minor cleavages (not indicated by triangles) are temporary.

species. A childless organism is excluded from being in any infinitary species (e.g., by Proposition 5); this is reminiscent of the cladist’s disregard for the sterile mule. Even if an organism has infinitely many descendants, it is still no guarantee of belonging to an infinitary species (see Section 6.1). Third, when an organism does have a species, it might not be unique: an individual may belong to multiple infinitary species at once (but the magnitude of this flaw is limited by Proposition 8). These crucial flaws re-emphasize that while normal species are like nodes on the tree of life, infinitary species are more like “leaves at infinity.”

We compared and contrasted our new infinitary species notion with the internodal species concept of Hennig, as formalized by Kornet et al. To contrast the two, we compared how they performed on a particularly extreme population— a technique which we referred to as using a *benchmark population*, and which we hope might serve as a more general application of infinitary graph theory to the species problem, breaking it into more manageable species subproblems.

We’ve exhibited some new theorems (among them, a dualization of the Knight-Darwin Law) which we find interesting in their own right. These theorems, like those of Kornet et al. (1995) before us, are of a less computational nature than a lot of mathematical theorems which have come from biology. We hope they may contribute to the two-way bridge between biology and the theoretical, philosophical, combinatorial side of mathematics.

8 Acknowledgments

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A Proof of Theorem 12

In this appendix we will prove Theorem 12 (hereafter we assume its hypotheses). First we review the definitions in Kornet et al. (1995). As we state them they are not equivalent; they are altered to fit the hypotheses of Theorem 12, allowing us to simplify them⁸.

Definition 5. For any $u \in G$, write $\mathbb{DYN}(u)$ for the set $\{x \in G : u(\mathbf{PC}_{\geq u})x\}$ and write $\geq (u)$ for $\{x \in G : t(x) > t(u)\}$. If $u, v \in G$ and $t(u) < t(v)$, define

$$u\mathbf{INT}v :\Leftrightarrow u(\mathbf{PC}_{\geq u})v \wedge \forall r[\{u(\mathbf{PC}_{\geq u})r \wedge (t(r) \leq t(v))\} \Rightarrow (\mathbb{DYN}(u) \cap \geq (r) = \mathbb{DYN}(r))].$$

If $t(v) < t(u)$ then $u\mathbf{INT}v :\Leftrightarrow v\mathbf{INT}u$, and if $t(v) = t(u)$ then $u = v$ by our assumption that no individuals are born simultaneously, and we define $u\mathbf{INT}u$.

The main theorem of Kornet et al. (1995) implies \mathbf{INT} is an equivalence relation.

Definition 6. An *internodon* is an \mathbf{INT} -equivalence class.

We could now dive directly into the proof of Theorem 12 but we prefer to factor out a sufficient condition which might be useful in the future for proving that other species notions decompose into internodons (this condition, too, will be generalized in future work).

Proposition 13. (Sufficient conditions for internodons-decomposition) (Assuming the hypotheses of Theorem 12.) Let $S \subseteq V$. If S is undirancestrally closed, and for each $u \in S$ and $t \in \mathbb{R}$ there is some $u' \in S$ born after t with $u(\mathbf{PC}_{\geq u})u'$; then S is a union of internodons.

Proof. It suffices to let $u \in S$, $v \in G$, and show that if $u\mathbf{INT}v$ then $v \in S$.

Case 1: v is born before u . Since $v\mathbf{INT}u$, in particular $v(\mathbf{PC}_{\geq v})u$. Thus v is an undirancestor of u , putting $v \in S$ by undirancestral closure.

Case 2: v is born after u . Since $u\mathbf{INT}v$, by definition of \mathbf{INT} we have $u(\mathbf{PC}_{\geq u})v$ and (*) for every r such that $u(\mathbf{PC}_{\geq u})r$ and $t(r) \leq t(v)$, we have $\mathbb{DYN}(u) \cap \geq (r) = \mathbb{DYN}(r)$.

⁸To be precise, we are assuming that every individual has the \mathbf{SD} property, which equates the equivalence relations \mathbf{INT} and \mathbf{INTSD} , as well as the sets \mathbb{DYN} and \mathbb{GDYN} , of the 1995 paper.

By the proposition’s hypothesis, there is some $u' \in S$, born after v , such that $u(\mathbf{PC}_{\geq u})u'$. Letting $r = v$ in (*), we see (since $u(\mathbf{PC}_{\geq u})v$ and $t(v) \leq t(v)$) that $\mathbb{DYN}(u) \cap \geq (v) = \mathbb{DYN}(v)$. Since $u' \in \mathbb{DYN}(u) \cap \geq (v)$, this shows $u' \in \mathbb{DYN}(v)$, that is, $v(\mathbf{PC}_{\geq v})u'$. Thus v is an undirancestor of u' , so $v \in S$ by undirancestral closure of S . \square

Proof of Theorem 12. Let S be an inspecies (type II). The first hypothesis of Proposition 13 holds since S is undirancestrally closed by definition. The second hypothesis of Proposition 13 is immediate by Proposition 6. \square

The reader will have noticed that despite imposing such onerous hypotheses on Theorem 12, we barely seem to have actually used those hypotheses. Their key use was in simplifying the definition of internodons.

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