

Niche versus chance and tree diversity in forest gaps

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Why have so many ecologists been concerned with gap dynamics in forests? One compelling reason is that gap dynamics might promote the coexistence of competing tree species and thus help explain tree diversity. Gap dynamics is the process by which one or a few trees die, leaving a gap in the forest canopy that is then filled by other trees. Our question is: how much does niche partitioning (specialization on different resources), versus chance events of tree establishment, contribute to the diversity of trees regenerating in gaps (Box 1)¹? Because gap dynamics characterize all mature forests², the answer might elucidate the temperate–tropical gradient in tree species richness. More generally, the answer would increase our understanding of how much ecological communities consist of coadapted species occupying different niches or of chance collections of species behaving individualistically³.

The death of an adult tree creates a forest gap in which light and soil resources are available for saplings or colonizing seedlings. Because most species depend on gaps for regeneration^{4,5}, they might compete for, and partition, gap resources. For example, if light and soil resources vary predictably within and among gaps, competition could lead to specialization on different levels of these resources^{4,6}. Furthermore, with steeper sun angles and presumed lower soil fertility in the tropics, contrasts along the resource gradient from shaded understory to gap center might be greater in tropical than temperate forests⁷. Gaps might also be more frequent in the tropics⁴. Partitioning of more greatly contrasting and frequently created resources in tropical gaps might help maintain higher tree diversity there.

To demonstrate coexistence via niche partitioning in gaps, we must confirm three premises: there is a gradient in the availability of crucial resources in gaps; tree species perform differently along this gradient; and these differences contribute to species coexistence⁸. If any of these premises are false, it suggests an important role for chance events in determining gap composition and tree diversity (Box 1).

Potential for niche partitioning in gaps

Concerning the first premise stated above, gaps do create gradients of resources crucial for trees. For example, light is generally greater in large gaps than in small gaps, and light generally decreases along a gradient from the gap center to the gap edge to intact forest understory^{9–11}. This applies at all latitudes; however, because sun angles

Studies that are unprecedented in scale, detail or approach show that niche partitioning contributes less, and chance events more, than expected to maintaining tree species richness via gap dynamics in tropical and temperate forests. Some tree species are differentially adapted for regeneration in different gap microenvironments. However, the stochastic availability of gaps, and limited recruitment of juveniles, mean that gaps are filled mostly by chance occupants rather than by best adapted species. This chance survival can slow competitive exclusion and maintain tree diversity. Gap dynamics do not explain the latitudinal gradient in tree richness.

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are lower in the temperate zone, direct light is less in the temperate gaps but reaches further into the surrounding understory¹².

The second premise is largely valid. In controlled studies in both tropical^{13–15} and temperate forests^{5,16,17}, many tree species do perform differently along resource gradients characteristic of the gap–understory continuum, but some species do not¹⁸. The differences in performance involve establishment, growth and survival (Figs 1 and 2), and result from physiological and morphological mechanisms^{8–10,17–19}. These studies focused on just a few species. However, in tropical Panama 118 species in a 50-hectare (ha) plot formed an array of interspecific differences in growth and survival, which suggests different adaptations to resource levels among many species, although clustered points in the array indicate strong similarity among others³. Nonetheless, given the overall array, plus other possible axes of variation in adaptations and gap environments, the scope for niche partitioning along gap–understory gradients is large^{20–22}.

Little partitioning is observed in gaps

However, the third premise is minimally valid. In the field, trees do not show enough differences in distribution or behavior to suggest that coexistence of many species is maintained via niche partitioning in gaps. In a Hawaiian forest with only two tree species, one species specializes on large gaps and the other on small gaps²³, but in some richer sites, at various latitudes, there was no evidence of gap partitioning^{24,25}. More typically, in both tropical and temperate forests, a few species occur preferentially on different substrates within gaps^{5,26–28} or at certain points along the gap size or gap–understory gradient. For example, light-demanding pioneers often occur in large gaps and gap centers^{17,19,28–34}. But, most species overlap too much on the gradient to indicate substantial partitioning.

However, many tropical studies have not been large enough in space, time, number of species and variety of tree size classes to test for partitioning at appropriate scales. For example, among size classes partitioning in gaps might operate for saplings but not seedlings, or vice versa³⁵. Work in Central America corrects these scale problems – it looks at the performance of trees in a range of sizes, over time, and relative to a variety of light and canopy environments in the field, but these studies still find little partitioning^{36–39}. In a Costa Rican forest, larger stems of 90 out of 104 tree species [stems ≥ 10 cm diameter

Box 1. Niche and chance effects in gaps: pertinent concepts

- Niche-based explanations of species coexistence

Traditional theory holds that plant species occupy niches partitioned by resource or habitat differentiation. **Niche partitioning** reduces interspecific competition and permits coexistence. However, as adults, coexisting tree species often appear to occupy similar niches. In this case, the **regeneration niche**, 'an expression of the requirements for a high chance of success in the replacement of one mature individual by a new mature individual'⁴⁹, might explain coexistence. Thus niche partitioning can be limited to the regeneration stage of tree life histories. In forests, canopy gaps are important sites for tree regeneration that might provide spatial gradients for resource or habitat differentiation. **Gap partitioning** occurs when species differentiate along gradients within gaps or among gaps of different size.

- Other explanations of species coexistence

Regardless of niche relationships, the **density effect** maintains diversity in gaps simply because gaps are sites with high densities of juvenile stems and, therefore, they tend to have high species richness⁴⁰. As explained further in this review, **chance** events of gap creation and tree regeneration could maintain diversity of species with similar regeneration requirements. The creation of gap sites important for regeneration is essentially stochastic within a forest, and the seeds or juveniles present in a gap can vary greatly depending on the vagaries and limits to seed dispersal and establishment in space and time, and regardless of gap characteristics. Because of this **recruitment limitation** ('the failure of a species to recruit in all sites favorable for its growth and survival'³⁹), gaps are occupied not by the best competitor for a particular site but by a subset of species that simply happens to be present.

If chance, rather than differences in competitive ability, controls abundances a **community drift model projects** the effects on species coexistence and diversity^{3,45}. Given a maximum number of individual trees in a community, and equal per capita probabilities of birth and death among species, rates of turnover in individual trees generally do not lead to rapid extinction of species. Although small populations are more prone to extinction, projected population persistence times are adequate to maintain their presence and community diversity.

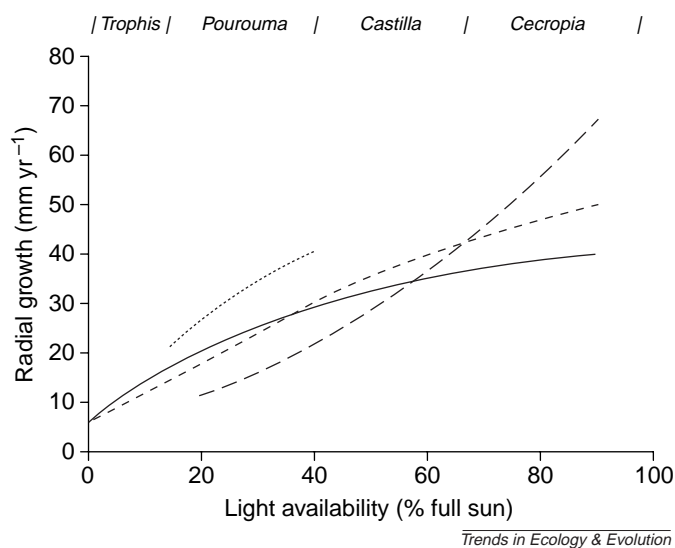


Fig. 1. Effects of light levels on growth (curves) and projected dominance (top row with dominance range by genus) of selected tree seedling species in a tropical forest in Costa Rica. Curves extend only over the range of light levels conferring adequate survivorship. Dominance is projected where survival is likely and growth is comparatively high. Species are *Trophis racemosa* (unbroken line), *Pourouma aspera* (dotted line), *Castilla elastica* (short dashed line), and *Cecropia obtusifolia* (long dashed line). Each species dominates in a different range of light availability. Reproduced, with permission, from Ref. 15.

at breast height (dbh) in 11 ha] were randomly distributed along the forest-wide gradient of light environments³⁶. Most species had centers of distribution in intermediate environments, and only 14 species were found mostly in either high or low light. In the Panamanian forest mentioned previously, saplings (stems 1–4 cm dbh) of 79 out of 108 tree and

shrub species responded as 'generalists' to canopy height (measured periodically above all points on a 5 m grid)³⁷. Generalists survived well and grew slowly in both low canopy (<10 m) and high canopy (≥10 m) forest, but recruited better under low canopy forests. Even the seedling abundances of light-demanding pioneer species, which would seem most sensitive to gap environments, were not directly related to gap size or light climate in newly formed gaps³⁸. All these results on populations contradict the hypothesis that species coexistence and diversity are maintained by niche diversification along a gap-created light gradient.

At the community level, if gaps promote tree species richness by providing a gradient of regeneration microsites of any resource, then: species richness on a per-stem basis should be greatest in areas of recent gap creation; relative abundances of species should change during regrowth in gaps, because species differentially respond to microsites; and species richness should increase with gap area, and at a faster rate than it increases with area in nongap forest, because large gaps should include more microsite heterogeneity than small gaps³⁹. These predictions were tested by Stephen Hubbell *et al.* in the 50-ha Panama plot³⁹. They monitored sapling (1–3.9 cm dbh) composition from 1985 to 1995 in approximately 430 gap areas (top of canopy initially <5 m high) present in 1983, and in nongap areas. The predictions were unsustainable. First, species richness of saplings was significantly higher in gap than nongap areas, but this was owing to higher stem densities in gaps; on a per-stem basis, gap and nongap areas were equally rich (Fig. 3). Second, relative abundances of most species in gaps did not change during the period – any changes were paralleled by similar changes for those species in nongap areas. Finally, total tree species richness increased with gap size, but not on a per-area or per-stem basis and not faster than it increases with area in nongap sites. In conclusion, gaps help maintain tree species diversity mostly by harboring higher densities of stems⁴⁰, not by providing more niches.

Gaps do essentially the same thing in a temperate forest in the Great Smoky Mountains, USA (Ref. 41). Here, it was predicted that if gap partitioning promotes diversity then species would accumulate more rapidly along the entire gradient from gap center to shaded understory, because the gradient should include numerous distinct niches, than along portions of the gradient entirely within gap or understory, presumably with limited niche variety. Also, the relative abundances of species in gaps would differ from those in the understory, and because large gaps should include more microsite heterogeneity than small gaps, relative abundances would differ among gaps of different sizes. To test these predictions, all trees >1.37 m tall and <10 cm dbh (10–15 species ha⁻¹) were censused in three 1-ha plots subdivided into 10 × 10 m quadrats – these were classified as gap, gap-border or nongap, depending on the predominant structure. The predictions were mostly unsustainable. Species–area curves were steepest in gap plots, but species–stem curves were similar among the entire gradient and all portions of it (Fig. 4). Except for a few pioneer species, the relative abundances of most species were similar between gaps and understory, and large gaps were richer in total species but not on a per-stem basis. As in the tropical Panamanian forest, gaps in this temperate forest promote species richness mostly by sustaining high stem densities, not by providing more niches.

How chance limits niche partitioning in gaps

Our review suggests that, in both tropical and temperate forest, gaps create a light gradient that tree species could

partition and that tested species perform differently along this gradient in controlled studies. Thus, the potential for niche partitioning exists. Some partitioning is evident, but is less than expected, and no comparisons indicate relatively more partitioning or more frequent gaps in tropical than in temperate forests. Although partitioning might be expected, chance can both limit partitioning and promote diversity in gaps. Chance manifests itself in the dominance of advance regeneration, in variable light conditions and in recruitment limitation. All three factors operate in both tropical and temperate forests.

Gap partitioning is rarely observed because gaps mostly contain advance regeneration, that is, juveniles of shade-tolerant species present in the understory before gap opening. Regrowth in gaps is often dominated simply by the tallest advance regenerators at that time^{11,24,28}; this is evident from direct observation and from the fact that overall gap composition changes little during regrowth^{32,34,39}. Thus, pre-gap patterns in the understory (where a given tree dies by chance), not postgap partitioning, largely determine gap composition³⁴.

Gap partitioning is also restricted by light levels that, along the average continuum, vary at particular points in heterogeneously structured gaps, and change with season and regrowth¹⁰⁻¹². Trees, being sessile, must be broadly adapted to cope with this chance variability; thus, distributions overlap on this irregular continuum and partitioning is unlikely²⁵. Exceptions prove the rule: partitioning in gaps is most evident among species that specialize on relatively fixed conditions of soil and topography^{26,36}.

Finally, gap partitioning would not evolve if limited ability to disperse to, and establish in, gaps allows them to be filled by chance assortments of whatever species are nearby, not by particular species repeatedly competing with each other for particular microsites. The seedling community representing the 314 species ≥ 1 cm dbh in the 50-ha Panama plot is both dispersal- and establishment-limited³⁹. During ten years, all seeds were identified in 200 traps in the plot. Among the 1.3×10^6 seeds trapped, no seeds were found for more than 50 species occurring on the plot as adults; half the species dispersed seeds to six or fewer traps; and only seven species dispersed seeds into more than 75% of the traps (Fig. 5). Already limited by dis-

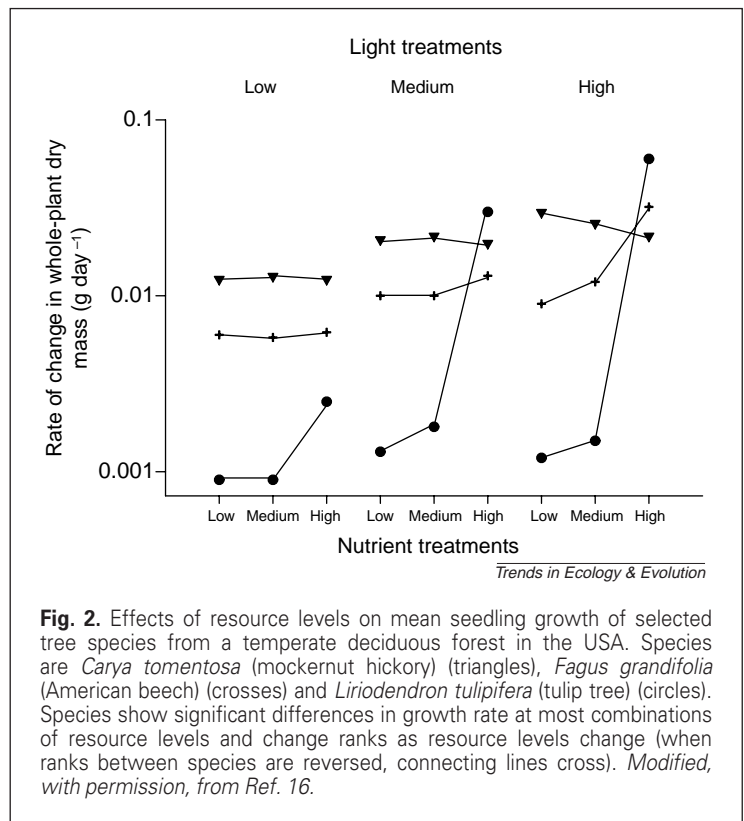


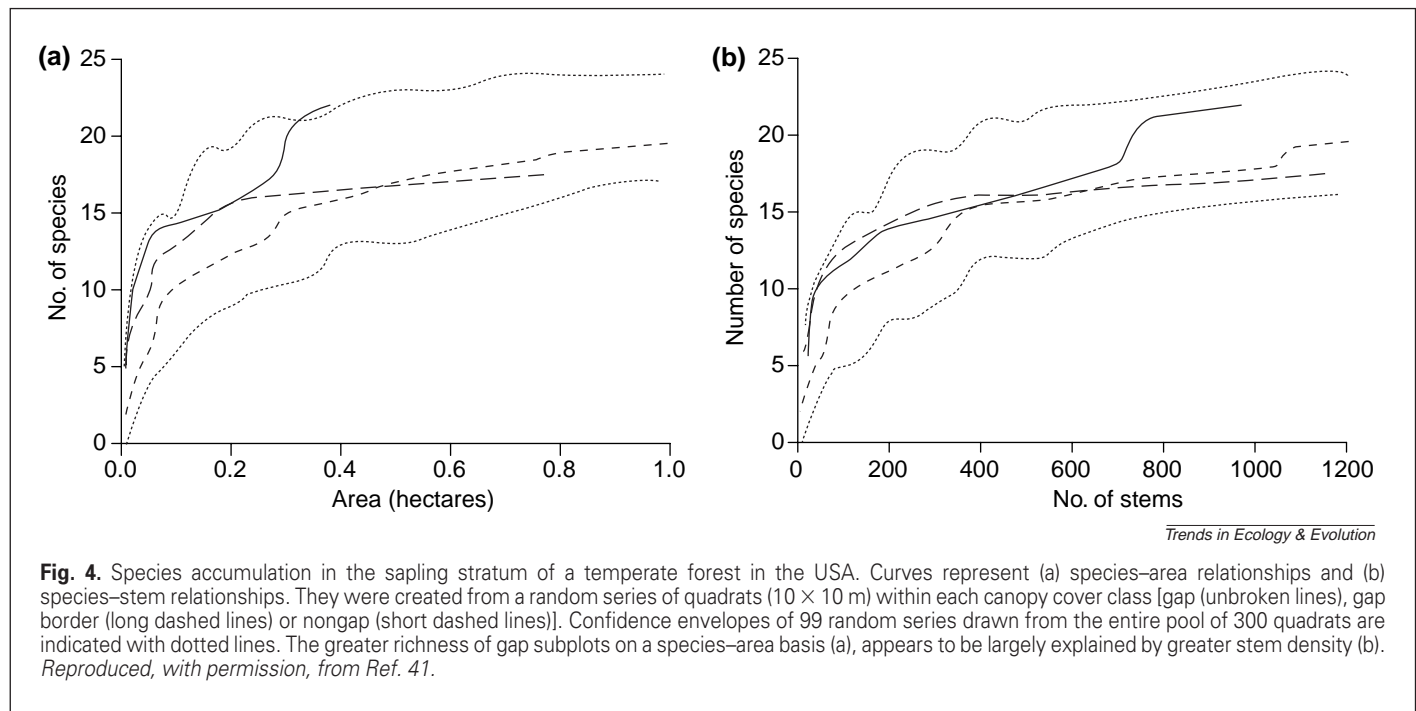
Fig. 2. Effects of resource levels on mean seedling growth of selected tree species from a temperate deciduous forest in the USA. Species are *Carya tomentosa* (mockernut hickory) (triangles), *Fagus grandifolia* (American beech) (crosses) and *Liriodendron tulipifera* (tulip tree) (circles). Species show significant differences in growth rate at most combinations of resource levels and change ranks as resource levels change (when ranks between species are reversed, connecting lines cross). Modified, with permission, from Ref. 16.

persal, establishment further restricts seedling composition. Seedlings in the plot were censused in 2000 1-m² subplots, and of the 314 species in the plot, only 136 were found as seedlings. Of these, the most frequent occupied only 14.9% of the subplots, while 74.3% occupied fewer than 1% of the subplots. Even seedlings of well-dispersed pioneers occupy only a small fraction of the gaps presumably suitable for their regeneration³⁸. In a Malaysian forest, the similarity of composition between intact forest and adjacent gaps, and between neighboring gaps, also suggested recruitment limitation²⁸.

We might expect less recruitment limitation in temperate forests, where lower species richness allows more adults (and propagules) per species in a given area. However,



Fig. 3. Cumulative distributions of species richness in the sapling stratum of a tropical forest in Panama. Quadrats (20 × 20 m) containing gaps are represented by unbroken lines. Those free of gaps are represented by dotted lines. (a) Distributions of species richness per quadrat. (b) Distributions of species richness per stem. The greater richness of gap quadrats, evident as species per quadrat (a), appears to be largely explained by greater stem density (i.e. species per quadrat per stem) (b). Reproduced, with permission, from Ref. 39. Copyright permission for electronic format not granted.



recruitment limitation is also indicated here by low seed rain⁵, by seedling communities that mainly reflect local adult abundances⁴² and, in one case, by the total lack of seedling establishment in suitable gaps⁴³. Scaling up, modeled field data suggest that limited recruitment strongly affects species abundances in a forest in Connecticut, USA (Ref. 44).

Chance, diversity and counterevidence

In the Panama plot, gaps typically include saplings of only about 2.3% of canopy species in the forest, mostly comprising whichever juveniles happen to be there when the gap forms. The probable winner among these is the tallest individual, rather than the species that is best adapted to that site³⁹. Thus, gap composition is largely determined by chance, not niche.

Because most species require growth in gaps to reach maturity, forest-wide relative abundances would also reflect chance. Indeed, patterns of relative abundance, modeled

solely on the basis of recruitment limitation, closely mimic observed abundance patterns in the Panama plot³. Recruitment limitation actually maintains diversity in community models; although it does not prevent the ultimate extinction of inferior competitors, the frequent chance success of inferiors delays their extinction for so long that speciation or immigration of new species from the larger region replace losses^{3,45}. Regional diversity of species sets forest stand diversity, which, in turn, sets diversity in gaps³, not the reverse.

A study at smaller spatial scales illustrates this relationship. In a New Zealand forest, plant species richness in single quadrats in gaps increased in proportion with overall gap richness; thus, local richness seemed to be controlled by regional richness, not by niche-limited species packing⁴⁶.

Nonetheless, some results contradict this null model in which species are ecologically equivalent and drift so slowly in abundance that diversity is maintained. If chance largely controls tree distributions and abundances then



Fig. 5. Results of a 10-yr study with 200 seed traps in a 50-ha plot in Panama. Of the 314 species in the plot, only 260 were trapped. Both (a) frequency distribution of the number of species caught per trap, and (b) the species ranking by number of traps catching at least one seed of the species suggest strong dispersal limitation. *Reproduced, with permission, from Ref. 39. Copyright permission for electronic format not granted.*

we would not expect tree communities even in the same floristic region, and with nearly identical histories and substrates, to be statistically similar in composition. However, mature stands of forest that are distant from each other and have developed after primary succession on floodplains in Peru are more similar to each other in the abundance of common tree species than would be expected at random⁴⁷. This implies that biological 'assembly rules' involving niche, not chance, determine composition (but see critique in Ref. 3). Slowly drifting abundances are also questioned, because real mortality rates of many tree species are too high for them to persist long enough, merely through random dynamics, for speciation to offset extinction⁴⁸. These results do not invalidate the null model, so much as they confirm what most ecologists acknowledge: that tree communities are both niche- and chance-determined in some variable proportion^{1,3}.

A unity of process in tropical and temperate forest gaps

Ecologists were right to be concerned with gap dynamics. They have demonstrated, in both tropical and temperate forests, that gaps significantly affect forest architecture and environment, influence growth and reproduction of plants, and affect animal distributions. Gaps also help maintain tree diversity through the density effect and some niche partitioning, and, in particular, the chance occurrence of gaps interacts with recruitment limitation to permit species coexistence. Most importantly, these ecologists have demonstrated the predicted unity of process in gap dynamics among all forests², a process that includes both niche and chance effects. Being common to all forests, and similar in process, gap dynamics therefore cannot explain the latitudinal diversity gradient³⁹.

Prospects

Obviously, tree species can partition more than gaps²¹. The challenge is to discover the relative importance of niche versus chance along various gradients in ecological communities¹. The results are important for conservation practice and ecological theory. If chance plays a major role in forest composition, large, linked areas must be protected to conserve communities drifting in composition. If chance largely controls composition, are many distinctive characteristics of tree species selectively equivalent? If some species are ecologically equivalent, what is the function of this redundancy in ecosystems? The studies reviewed here might have settled some questions about niche, chance and diversity in gaps, but they raise other, perhaps more perplexing, issues.

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Evolution of the avian sex chromosomes and their role in sex determination

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It has long been known that the Y chromosome is crucial for development of the male phenotype in mammals. Intensive search for the testis-determining factor culminated in the early 1990s with the identification of the Y-linked *Sry* gene¹, present on the Y chromosome of most mammalian species studied so far. *Sry* triggers a cascade of proteins involved in male development that are encoded by autosomal, as well as X- and Y-linked, genes. However, the role of *Sry* as the key to sex differentiation does not extend outside mammals². For instance, birds appear to have a different system for sex differentiation, although the knowledge of how this system operates is lagging far behind what we know about mammals. Importantly, avian sex chromosomes show a reversed organization compared with mammals, females being heterogametic ZW and males homogametic ZZ. A long-standing issue in avian genetics has been whether the W chromosome is crucial for female development or whether it is the number of Z chromosomes that regulates male development³. The sex chromosome aneuploids (Box 1) required to answer this question have yet to be identified, but recent molecular analyses and gene mapping data have given the first hints

Is it the female-specific W chromosome of birds that causes the avian embryo to develop a female phenotype, analogous to the dominance mode of genic sex differentiation seen in mammals? Or is it the number of Z chromosomes that triggers male development, similar to the balance mode of differentiation seen in *Drosophila* and *Caenorhabditis elegans*? Although definite answers to these questions cannot be given yet, some recent data have provided support for the latter hypothesis. Moreover, despite the potentially common features of sex determination in mammals and birds, comparative mapping shows that the avian sex chromosomes have a different autosomal origin than the mammalian X and Y chromosomes.

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to the process of avian sex determination. Moreover, these new data give insights into the evolution of heteromorphic sex chromosomes in general, and in birds in particular. Here, I will discuss these recent achievements and make comparisons with mammals, birds' closest relatives, for which detailed knowledge on sex differentiation processes is available.

The avian sex chromosomes

The Z and W chromosomes of birds share many features with mammalian X and Y chromosomes, respectively. Both avian sex chromosomes are metacentric. They pair during meiosis and a synaptonemal complex (Box 1) is formed at the end of the short arms of the two chromosomes; therefore, a small pseudoautosomal region (Box 1) exists. Typically, the Z chromosome is

comparable in size with the fourth or the fifth chromosome pair, constituting some 7–10% of the total genome size⁴ (which in birds is only one-third of that in mammals). In most species, the W chromosome is considerably smaller and, without appropriate staining techniques, is sometimes difficult to distinguish from the many microchromosomes. In some species, from taxa as diverse as Piciformes,