significant long-term changes in nutrient mineralization, which causes major and often unexpected changes in plant species composition. Combined with Foster and Gross's observation about the strong effects of litter on plant species establishment, these results imply that litter production and decomposition must be considered if we are to understand the long-term dynamics of plant communities.

We are only just beginning to understand how litter-mediated mechanisms might determine species composition and diversity of plant communities. Effects of accumulated litter on the light intensity and spectral composition experienced by seeds and seedlings are certainly important, but there are many other effects that should also be taken into account. For example, we should consider the effects of litter on air humidity and pathogen transfer and the subsequent implications for seedling survival. We also need to know more about how changes in the quantities and chemical composition of the litter produced affect the accumulation of soil organic matter. Changes in the dynamics of soil organic matter could strongly affect nutrient mineralization and soil acidity, which are among the most important factors that determine the diversity in species-rich communities.

Acknowledgements
Thanks are due to Dr H. de Kroon for his comments on this article.

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Using integrative biology to explore constraints on evolution

Evolutionary biologists have long appreciated that enhancement of one trait during development might alter the expression of other correlated traits. Some effects might be positive; for example when physical activity increases skeletal mass, makes the heart more fit, and leads to greater coordination. A hoped-for positive correlation among cognitive abilities lies behind the recent fascination with the 'Mozart effect', whereby stimulating infants with appropriate music will lead to increased mathematical and spatial abilities. Banking on the Mozart effect to boost test scores in their states, the Florida legislature in the USA is considering a bill to require all child-care facilities to play 30 minutes of classical music each day and, in Georgia (USA), Governor Zell Miller is suggesting that all babies be sent home from the hospital with tapes of musical masters (apparently 20th century music will not be included).

Proponents of the Mozart effect might be disquieted to learn that evolutionary biologists expect that negative correlations will also be pervasive in biological systems. Because internal resources are limited, it has been speculated since Darwin that enhanced expression of one trait might result in diminished expression of others. Such constraints on development are expected whether the enhancement is caused by environmental factors or by genetic variation. Although tradeoffs between morphological traits during development have been anticipated, there has been surprisingly little empirical support for this notion. A recent set of experiments[1] employing genetic, endocrine, developmental and environmental manipulations of a butterfly (*Precis coenia*) and a scarab beetle (*Onthophagus taurus*) by Nijhout and Emlen, provides a convincing case for such morphological tradeoffs. The integrative approach employed in this study might also provide the means to explore whether the pathways of evolution are narrow or broad.

In *P. coenia* the imaginal disc that gives rise to the hindwings was removed from first instar larvae. This manipulation produced adults that had larger forewings than did sham-operated controls. Nijhout and Emlen interpret this to suggest that

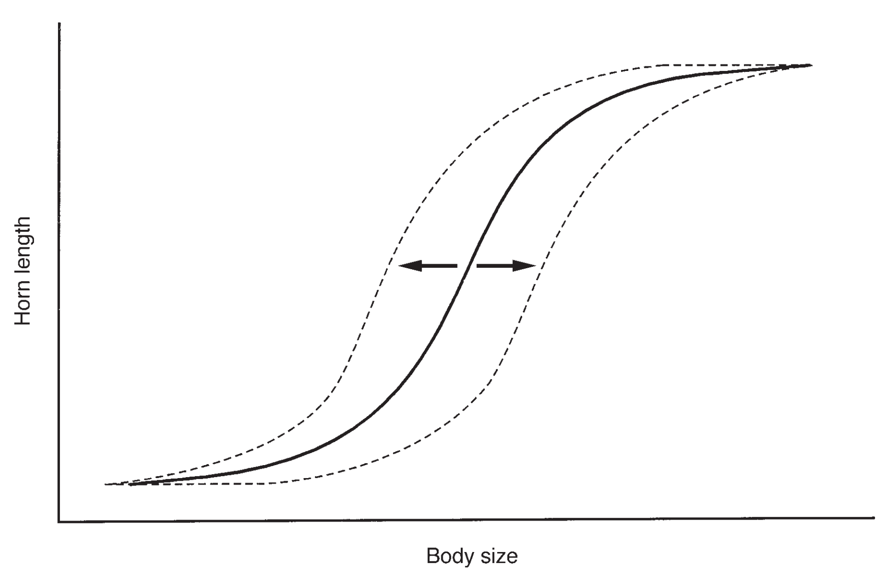

Fig. 1. The sigmoidal relationship between horn length and body size in *Onthophagus* (scarab) spp. results in large males with large horns and small males that are hornless[3]. The arrows represent the hypothesized most probable paths of evolutionary change. Selection experiments, as well as comparisons among species, suggest that lateral movement of the sigmoidal curve is much more likely during evolution than change in the shape of the curve.

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hind- and forewings in *P. coenia*, which develop in close proximity, compete for a common pool of internal resources during the larval to adult transition.

Competition between morphological structures was investigated from several angles in the scarab *O. taurus*, which exhibits male dimorphism in horn size (larger individuals possess well developed horns, whereas small individuals are hornless). Natural populations produce few males with intermediate-sized horns as a result of the sigmoidal relationship between horn and body size (Fig. 1). The ecological advantage of this dimorphism seems clear. Only large males will be able to guard and defend the burrows the females use to bury brood balls. Small, hornless males avoid direct male–male contact by digging bypass tunnels to intercept females underground. Emlen altered the horn-size:body-size relationship in two very different ways. Application of a single dose of methoprene (an analog of juvenile hormone) during the third instar produced hornless males where well developed horns would normally be expected. Males with endocrinologically-induced horn reduction, however, showed a compensatory increase in the size of their compound eyes. Compound eyes develop in close proximity to horns, and again, competition for resources between these two developing structures might account for the tradeoff. As in *P. coenia*, the size of more distant body parts was not affected by the manipulation.

Artificial selection was employed for seven generations to effect a similar change in *O. acuminatus*. Males were selected for increased horn size for a given body size in one line and for decreased horn size in another line. Individuals in the long-horn selected line had smaller eyes than males in the small horn line (males of equal body size were compared), which is evidence of a negative genetic correlation between these two traits. Taken together, these two manipulations of *Onthophagus* spp. suggest a direct link between the developmental process and a genetic constraint.

It is likely that using different investigative techniques will provide further evidence to reinforce these results and will also enable evolutionary biologists to examine more clearly the possible evolutionary pathways and constraints in development. Nijhout and Emlen were pleased that both the genetic and hormonal manipulations of beetle horns produced a similar magnitude of change in the size of compound eyes. While many biologists spend a career employing only one or two potential research strategies, Emlen has undertaken studies employing four types of manipulation (manipulation of diet[2,3] and preliminary comparative analyses[4] were detailed in earlier studies). If the findings from all these studies are integrated, the implication is that the sigmoidal relationship between horn size and body size might be difficult to alter, whereas lateral movement of the entire curve represents a more probable evolutionary pathway (Fig. 1).

Anthony Zera has also taken a diverse research approach in his studies of wing length and migratory behavior of crickets. Like Emlen, Zera has exploited several advantages of working with insects, such as being able to breed large numbers of individuals over a short period and manipulate hormone levels by noninvasive topical applications. In *Gryllus firmus*, a crowded social environment or application of juvenile hormone (JH) during juvenile stages can induce short-winged adults and nonmigratory behavior[5]. Even the typically monomorphic long-winged *G. assimilis* will develop short wings, reduced flight muscles and larger ovaries in response to application of JH analogs, producing a manipulated phenotype that does not occur naturally[6]. Such hormonal engineering[7] could be useful for examining incipient stages of life-history evolution.

Interestingly, Zera and his colleagues have also directly selected for high and low activity of JH esterase, an enzyme that degrades JH and consequently reduces levels of JH in the blood. Selection on JH esterase activity produces strong within-stage correlated responses in its activity (juvenile–juvenile or adult–adult) but weak across-stage correlations (juvenile–adult)[8]. This suggests that selection for altered endocrine activity during one stage of development might not produce by-product effects that would constrain directional selection. This work might be the only example to date in which selection was imposed directly on an endocrine process. Such manipulations will probably be important for exploring the flexibility of physiology during evolutionary change.

Perhaps the most intriguing possibility for integrative research on insects is comparative work on the evolution of social behavior. Among the insects, numerous independent lineages, employing similar endocrine structures, have evolved parental as well as more advanced social behavior. It would be interesting to know if convergent social behavior is tied to convergent physiology. We might then be able to address whether physiological processes are extremely malleable under selection or whether the inherited physiology imposes formidable constraints.

By contrast, in other taxa, key social innovations might have evolved only a few times, making it difficult to examine whether alternative physiological routes could have accomplished the same functional change. Among mammals, for example, lactation probably evolved only once, making it impossible to determine whether divergent physiological pathways could have produced this change.

Behavioral and morphological tradeoffs occur because expressed traits are dependent on a common physiology that has limited resources during development. It is therefore not surprising that genetic and environmental effects acting on multiple traits interact in a complex way. An integrated research program, as exemplified by the work of Emlen, Nijhout, and Zera, will provide biologists with important tools for understanding how the resulting tradeoffs constrain evolution.

Acknowledgements
The author is supported by NSF grant 9420985.

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