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New Idea

The soil mosaic hypothesis: a synthesis of multi-trophic diversification via soil heterogeneity

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Abstract

Myriad unexplored mechanisms potentially drive ecological speciation and could help explain global variation in diversity. Here, we develop a novel hypothesis focused on variation in biotic, chemical, and physical properties of soil as a factor contributing to diversification in communities of plants and animals. The Soil Mosaic Hypothesis (SMH) suggests that differences in soil attributes can affect intraspecific variation in phytochemistry, leading to cascading ecological and evolutionary effects on higher trophic levels. To illustrate the potential importance of the SMH, we examine three underlying ideas: (1) plant species and species assemblages shift over time, exposing them to novel soil environments, which can lead to genetic differentiation; (2) differences in soil properties can alter phytochemistry via plasticity and local adaptation; (3) phytochemistry can drive herbivore diversification via divergent natural selection (i.e. ecological speciation). The SMH provides insight into the process of diversification in a variety of landscapes and at a variety of scales and may inform analyses of diversification at local, regional, and global scales.

Keywords: soil mosaics, diversification, phytochemistry, plant-animal interactions, resource availability, ecological speciation.

Introduction

The idea that ecological interactions can influence evolution has been a major component of evolutionary theory since Darwin developed the concept of natural selection (Darwin 1859), and it is clear that ecologically-based divergent natural selection is an important model of speciation (*reviewed by* Rundle and Nosil 2005, Nosil 2012). Ecological speciation occurs when populations are exposed to contrasting environments and ecologically-based divergent natural selection promotes (either directly or indirectly) the evolution of reproductive isolation. Divergent selection can result in differences in morphology, behavior, or other phenotypes, potentially leading to genetic isolation between populations comprised of ecologically specialized individuals (Schluter and McPhail 1992, Rundle and Nosil 2005, Matsubayashi et al. 2010, Soria-Carrasco et al. 2014). Research on ecological speciation has benefited from detailed studies of well-understood populations or taxa associated with different resources or habitats (e.g., Schluter and McPhail 1992, Rundle et al. 2000, Nosil et al. 2008, Matsubayashi et al. 2010, Nosil 2012, Soria-Carrasco et al. 2014), but there are still many unexplored axes of ecological variation that potentially contribute to diversification (Coley et al. 1985, Thompson 2005, Whitham et al. 2008, Dyer et al. 2014). Here, we consider a previously understudied potential source of divergent natural selection: variation in soils and associated effects on phytochemistry and plant and animal community structure.

The Soil Mosaic Hypothesis (SMH) posits that differences in soil properties (i.e. biotic, chemical and physical factors) can affect individual variation in plant primary and secondary metabolites, yielding a highly variable phytochemical landscape (*sensu* Hunter 2016) and leading to cascading ecological and evolutionary effects on autotroph and consumer trophic levels. Soil heterogeneity could lead by direct and indirect mechanisms to reproductive isolation in plant and herbivore populations. A direct mechanism could be, for example, adaptation by herbivores to plant populations with divergent phenology causing a shift in herbivore phenology (emergence time or peak abundance) that immediately isolates consumer populations. A less direct mechanism could be local adaptation to phytochemistry, and associated selection against hybrids that are maladapted to either of the chemical profiles experienced by the parents. The SMH is not entirely novel: in addition to theories of ecological speciation and host-associated differentiation (Stireman et al. 2005), the SMH can be considered a corollary to the following well-established theories: *i*) coevolution (Ehrlich and Raven 1964, Berenbaum and Feeny 1981, Agrawal et al. 2012), *ii*) the geographic mosaic (Thompson 1999, Thompson 2005), *iii*) plant defense theory (Bryant et al. 1983, Coley et al. 1985, Stamp 2003, Massad et al. 2011, Smilanich et al. 2016), *iv*) effects of environmental heterogeneity on communities and ecosystems (Ricklefs 1977, Whitham et al. 2006, 2008), *v*) the phytochemical landscape (Hunter 2016), and *vi*) plant-soil feedbacks (van Breeman and Finzi 1998, van der Putten et al. 2013, Schweitzer et al. 2014). The utility of the SMH is that it utilizes key components of existing theory that are usually limited in scope to average levels of chemical defense and bi-trophic interactions to provide a focused, testable framework that includes a new perspective on phytochemical diversity, multi-trophic interactions, and abiotic selective drivers of diversification. Natural systems are adaptive landscapes of complex community dynamics. The SMH integrates both below- and above-ground processes when assessing patterns of ecological divergence and speciation. We examine three underlying postulates (Figure 1): (1) plant species and communities are exposed to diverse soil environments across multiple spatial and temporal scales, which can lead to divergence in plant populations; (2) differences in soil properties can alter plant primary and secondary metabolites; and (3) variation in phytochemistry can drive herbivore diversification via ecological speciation at fine geographic scales.

While these postulates could be used to help understand the link between soils, phytochemistry, and diversification in any ecosystem, such mechanistic relationships may be particularly evident in regions that encompass extreme habitat variation (e.g., serpentine soils, white-sands versus clay soils, dry versus wet tropical forests, or mountains) and which have a unique combination of soil diversity, movement dynamics, and biotic interactions. Below we will discuss each of the three aspects of the SMH to illuminate the process by which consumers adapt to phytochemical variation driven by changes in soil chemical and physical properties.

1. Plants disperse to novel soil environments.

Because the chemical and physical properties of soil are influenced by associated climate, parent material, topography, time, and biotic communities (Laliberté et al. 2013, van der Putten et al. 2013), distinct soil types can occur in close proximity, leading to a soil mosaic (Sollins et al. 1994). Soil mosaics characterize many landscapes at different spatial scales, and soil formation models predict that tropical soils in particular should have extreme heterogeneity in soil properties (e.g., Jenny 1980).

When plant ranges shift due to climatic changes or other factors, populations are likely to encounter novel soils because of the heterogeneity of most soil landscapes. Ecological processes that promote dispersal will also lead to an increased likelihood that a plant will

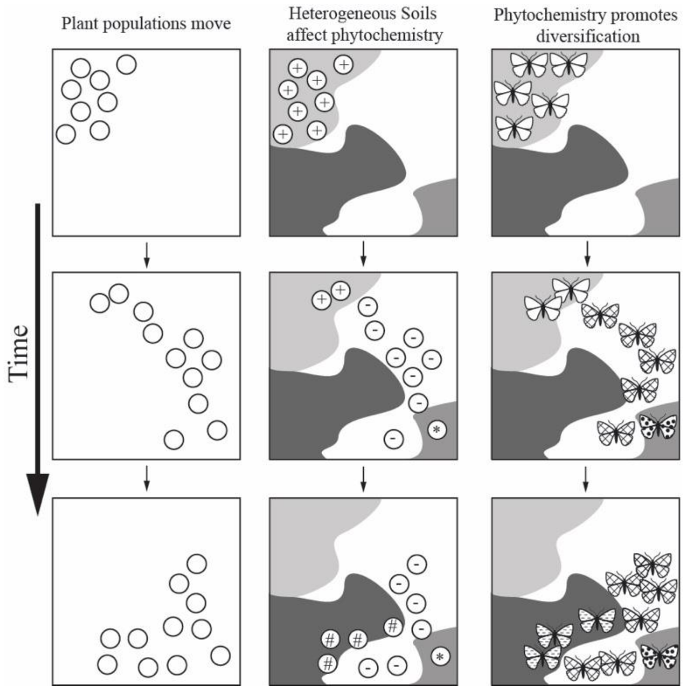

Figure 1. A graphical model of the Soil Mosaic Hypothesis: 1) Soils are heterogeneous and plant populations move; 2) Soils affect phytochemistry, creating subpopulations with different chemistry; 3) Phytochemistry affects herbivore diversification. The *first column* shows that plants (open circles) move across a landscape over time. The *second column* shows how soils with distinct characteristics (shaded regions) influence plant phytochemistry. Plastic changes in phytochemistry are represented by different symbols within each circle – these changes can also be followed by genetic assimilation. The *third column* shows how herbivores track the movement of plant subpopulations over time. The pattern on the wings of the herbivores represents divergent characters that are linked to adaptations to unique phytochemical profiles of associated host plants.

disperse onto a soil with attributes that are different from the parent plant. Neotropical trees, for example, often experience long distance dispersal (Ward et al. 2005). The lowland tapir, *Tapirus terrestris*, acts as an important long distance disperser of the tropical palm *Maximiliana maripa*. Tapirs disperse palm seeds as far away as 2 km from parent trees, increasing survival rates of seeds to 98% for those that are dispersed compared to 17% for seeds close to parent trees (Fragoso 1997; Fragoso et al. 2003). Long distance dispersal events increase the probability of offspring shifting to a different soil type than the parent and could result in offspring with different phytochemical or nutritional properties from their parents, leading to increased morphological and genetic divergence (e.g., Barbosa et al. 2013, Misiewicz and Fine 2014).

2. Soils affect phytochemistry.

Changes in biotic and abiotic factors, including soil microbes and nutrients, are known to cause significant changes in plant chemistry, and the magnitude of these changes are likely to affect many biotic interactions that are mediated by chemistry (Hunter and Price 1992, van Breeman and Finzi 1998, Dyer et al. 2004, Massad and Dyer 2010). There is a vast literature on the plasticity of plant secondary metabolites, and while there is little consensus on the directions and magnitudes of these responses to changes in soil nutrients, there is ample evidence of large shifts in phytochemical profiles in response to soil nutrient variation *(reviewed by* Massad et al. 2012).

Phytochemical diversity maintains plant function and fitness across diverse environments, affecting herbivore communities (Richards et al. 2015, Glassmire et al. 2016) and habitat specialization by plants (Fine et al. 2013). Phytochemical plasticity could be more beneficial when there are resource pulses or outbreaks of herbivory in resource-limited environments, and empirical studies have shown that plants allocate more resources to defense versus growth under such conditions to prevent the loss of leaf tissue, which is costly to replace (*reviewed in* Endara & Coley 2011). Thus, the adaptive nature of phytochemical plasticity can depend on resource availability and the presence of biotic interactions (Coley et al. 1985, Dyer et al. 2004, Hunter 2016). Similarly, the growth-defense trade-off hypothesis suggests plants have different phytochemical defense strategies across soil gradients (Coley et al. 1985), potentially promoting soil specialization and adaptation over evolutionary time (Fine et al. 2013).

Thus, soil mosaics can provide an adaptive landscape promoting edaphic specialization and plant diversification. For example, patterns of spatial genetic structure in the tropical tree *Protium subserratum* (Burseracae) in the Ducke Reserve Brazil are significantly influenced by soil type, which is highly heterogeneous, with soil clay composition ranging from 2% to 80% in a 250 m^2 area (Barbosa et al. 2013). Edaphic specialization has been posited as a mechanism of diversification for multiple plant lineages; two prominent examples are diversification of Protieae species (Burseraceae) shifting from clay to sand soils (Fine et al. 2005, Fine et al. 2014) and endemism of streptanthoid species (Brassicaceae) transitioning from bare to serpentine soils (Cacho and Strauss 2014). Furthermore, studies have shown that some populations of *Mimulus guttatus* monkeyflowers (Family: Phrymaceae) have adapted to the copper-rich soils near copper mines, resulting in ecological speciation (Macnair and Christie 1983).

3. Phytochemistry affects herbivore diversity.

While diversification in herbivorous insects is often thought to involve shifts in host plant use (e.g., Powell et al. 2013, Soria-Carrasco et al. 2014), recent evidence from a diverse tropical system raises the possibility that diversification can also occur without host shifts and also without major geographic barriers, supporting the hypothesis that intraspecific variation in phytochemistry may play a role in insect diversification at relatively small spatial scales (Wilson et al. 2012, Glassmire et al. 2016). Furthermore, intraspecific variation in edaphic-associated phytochemistry sheds light on the documented phenomenon that distinct insect communities are associated with soil ecotypes, as in *P. subserratum* (Fine et al. 2013). It is well known that phytochemical variation can influence insect herbivores by affecting oviposition preference (Carlsson et al. 2011), larval performance, mortality (Richards et al. 2010), and the ability of an herbivore to defend itself against predators and parasitoids (Smilanich et al. 2009). The SMH suggests that as plants experience new soil environments and respond with altered phytochemical properties, associated herbivore communities will experience strong selection pressure based on these new phytochemical environments, which can lead to diversification and speciation. Richards et al. (2015) found that phytochemical variation affects entire host-associated communities, including the diet breadth and diversity of herbivores.

Future Studies

The three main tenets of the SMH described here were inspired by pondering the theoretical framework of the phytochemical landscape (Hunter 2016) as well as considering our own work showing evidence of rapid diversification within one genus of herbivores (*Eois*, Geometridae: Larentiinae) that includes multiple sister species consuming the same host plant species in close geographic proximity (Wilson et al. 2012, Glassmire et al. 2016). The SMH incorporates a combination of ecological and evolutionary processes associated with plants colonizing novel soils, followed by diversification of taxa at higher trophic levels. Below we provide several examples of future studies that would test specific hypotheses generated by the SMH to elucidate how soil interacts in a multi-trophic framework.

First, transplant studies should be conducted to examine how differences in soil nutrient availability influence phytochemical profiles, and how this impacts performance of the associated arthropod communities (Fine et al. 2013). These studies should be accompanied by feeding assays to examine herbivore preference and performance on phytochemically distinct plants. Second, controlled experiments should investigate the mechanisms by which soil resource availability affects phytochemical plasticity in the presence of natural enemies. This would involve a fully-crossed experimental design including manipulated abiotic (addition of soil resources) and biotic factors (exclusion of herbivores and natural enemies). Associated with these manipulations of soil resources, the richness and abundance of soil biotic properties could be manipulated to examine the influence of soil biotic diversity on phytochemical diversity. For example, one could experimentally alter the diversity of arbuscular mycorrhizal fungi, bacteria, and soil arthropods, and quantify differences in phytochemistry. One important response variable for both types of soil manipulation experiments is the concentration of individual secondary metabolites, allowing for responses to these key questions: 1) How important are soil resources, arthropod communities, and the interaction between these factors for structuring plant secondary metabolomes? 2) What are the norms of reaction for individual secondary metabolites and phytochemical diversity in response to soil nutrients and arthropods? 3) Are any metabolites fixed with respect to variation in soil and arthropods? In experiments of this kind, arthropod communities can both be manipulated as treatments and measured as response variables, including behavior (e.g., oviposition preferences) of focal herbivores.

Finally, as an extension of the SMH, future studies could investigate the possibility of plant defensive profiles becoming fixed by genetic assimilation (Waddington 1953, Crispo 2007). If the colonization of a novel edaphic environment results in the developmentally-plastic production of a distinct phytochemical profile that is favored by natural selection, theory suggests that the novel phenotype could eventually become fixed because plasticity to produce that phenotype would be selected against at that location. An interesting outcome of this process would be the retention of phytochemical diversity at the species or meta-population scale (Figure 1), even in the face of range shifts associated with climatic fluctuations, since the previously plastic phenotype is fixed. The conversion from plasticity to fixed phytochemical diversity also opens the possibility for another mechanistic component of classic coevolutionary dynamics between plants and herbivores. While the potential importance of genetic assimilation for micro and macroevolutionary processes is well recognized (West-Eberhard 2003, Ehrenreich and Pfennig 2016), we know very little about the potential for assimilation to affect phytochemical phenotypes or associated arthropod communities. Perhaps the best systems for utilizing this approach would be well-resolved foundation species, such as *Populus*, for which there are documented networks of interacting soil microbes and herbivore communities, as well as documented effects from genes to ecosystems (Whitham et al. 2006, 2008, Lau et al. 2016).

Conclusion

Variation in phytochemical profiles can arise in plants following the colonization of novel soil types (Fine et al. 2006, Fine et al. 2013, Cacho and Strauss 2014), allowing for phytochemically-associated adaptation and divergence to occur in herbivores at a fine geographic scale (Glassmire et al. 2016). Future studies investigating previously unrecognized mechanisms of diversification, such as the processes comprising the SMH, will shed light on the origin and maintenance of biodiversity. Testing this hypothesis should be a part of the general goal to understand the extent to which ecological processes influence diversification in a multi-trophic framework.

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References

Agrawal, A.A., Petschenka, G., Bingham, R.A., Weber, M.G. and S. Rasmann. 2012. Toxic cardenolides: chemical ecology and coevolution of specialized plant-herbivore interactions. New Phytologist 194: 28-45. CrossRef

Barbosa, C. E. A., Misiewicz, T.M., Fine, P. V. A. and F. R. C. Costa. 2013. Plant Ontogeny, Spatial Distance, and Soil Type Influence Patterns of Relatedness in a Common Amazonian Tree. PloS ONE 8: e62639. CrossRef

Berenbaum, M. and P. Feeny. 1981. Toxicity of angular furanocoumarins to swallowtail butterflies: escalation in a coevolutionary arms race? Science 212: 927-929. CrossRef

Bryant J.P., F.S. Chapin III, and D.R. Klein. 1983. Carbon/ nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357-368. CrossRef

Cacho, N. I. and S. Y. Strauss. 2014. Occupation of bare habitats, an evolutionary precursor to soil specialization in plants. PNAS 111: 15132-15137. CrossRef

Carlsson, M. A., Bisch-Knaden, S., Schäpers, A., Mozuraitis, R., Hansson, B. S. and N. Janz. 2011. Odour maps in the brain of butterflies with divergent host-plant preferences. PLoS ONE 6: e24025. CrossRef

Coley, P. D., Bryant, J. P. and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. Science 230: 895-899. CrossRef

Crispo, E. 2007. The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. Evolution 61: 2469-2479. CrossRef

Darwin, C. 1859. On the origin ofspecies by means of natural selection, or the preservation of favoured races in the struggle for life. Appleton and Company, New York, New York.

Dyer, L. A., Letourneau, D. K., Dodson, C. D., Tobler, M. A., Stireman, J. O. and A. Hsu. 2004. Ecological causes and consequences of variation in defensive chemistry of a Neotropical shrub. Ecology 85: 2795-2803. CrossRef

Dyer, L. A., Parchman, T. L., Jeffrey, C. S. and L. A. Richards. 2014. New dimensions of tropical diversity: an inordinate fondness for insect molecules, taxa, and trophic interactions. Current Opinion in Insect Science 2: 14-19. CrossRef

Ehrenreich, I.M. and D.W. Pfennig. 2016. Genetic assimilation: a review of its potential proximate causes and evolutionary consequences. Annals of Botany London, 117: 769-779. CrossRef

Ehrlich, P.R. and P.H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18: 586-608. CrossRef

Endara, M.J. and P.D. Coley. 2011. The resource availability hypothesis revisited: a meta-analysis. Functional Ecology, 25: 389-398. CrossRef

Fedorov, A.A. 1966. The structure of the tropical rain forest and speciation in the humid tropics. Journal of Ecology 54: 1-11. CrossRef

Fine, P.V.A., Daly, D.C. and K. M. Cameron. 2005. The contribution of edaphic heterogeneiyt to the evolution and diversity of burseracear trees in the western Amazon. Evolution 59: 1464-1478. CrossRef

Fine, P.V.A., Miller, Z.J., Mesones, I. , Irazuzta, S., Appel, H.M., Stevens, M.H.H., Saaksjarvi, I., Schultz, J.C. and P.D. Coley. 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. Ecology 87: S150-S162. CrossRef

Fine, P.V.A., Metz, M.R., Lokvam, J., Mesones, I., Zuñiga, J.M.A., Lamarre, G.P.A., Pilco, M.V. and C. Baraloto. 2013. Insect herbivores, chemical innovation, and the evolution of habitat specialization in Amazonian trees. Ecology 94: 1764-1775. CrossRef

Fine, P. V. A., Zapata, F. and D. C. Daly. 2014. Investigating processes of neotropical rain forest tree diversification by examining the evolution and historical biogeography of the Protieae (Burseraceae). Evolution 68: 1988-2004. CrossRef

Fragoso, J.M.V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. Journal of Ecology 85: 519-529. CrossRef

Fragoso, J.M.V., Silvius, K.M. and J.A. Correa. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology 84: 1998-2006. CrossRef

Glassmire, A.E., Jeffrey, C.S., Forister, M.L., Parchman, T.L., Nice, C.C., Jahner, J.P., et al. 2016. Intraspecific phytochemical varation shapes community and population structure for specialist caterpillars. New Phytologist 212: 208-219. CrossRef

Hunter, M. D. and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724-732.

Hunter, M. D. 2016. The phytochemical landscape: linking trophic interactions and nutrient dynamics. Princeton University Press, Princeton, New Jersey. CrossRef

Jenny, H. 1980. The soil resource: origin and behavior. Springer Science & Business Media, New York, New York. CrossRef

Laliberté, E., Grace, J.B., Huston, M.A., Lambers, H., Teste, F.P., Turner, B.L. and D.A. Wardle. 2013. How does pedogenesis drive plant diversity? Trends in Ecology and Evolution 28: 331-340. CrossRef

Lau, M.K., Keith, A.R., Borrett, S.R., Shuster, S.M. and T.G. Whitham. 2016. Genotypic variation in foundation species generates network structure that may drive community dynamics and evolution. Ecology, 97: 733-742.

Macnair, M.R. and P. Christie. 1983. Reproductive isolation as a pleiotropic effect of copper tolerance in *Mimulus guttatus*. Heredity 50: 295-302. CrossRef

Massad, T.J. and L.A. Dyer. 2010. A meta-analysis of the effects of global environmental change on plant-herbivore interactions. Arthropod-Plant Interactions 4: 181-188. CrossRef

Massad, T.J., Fincher, R.M., Smilanich, A.M. and L.A. Dyer. 2011. A quantitative evaluation of major plant defense hypotheses, nature versus nurture, and chemistry versus ants. Arthropod-Plant Interactions 5: 125-139. CrossRef

Massad, T. J., Dyer, L.A. and G. Vega. 2012. Costs of defense and a test of the carbon-nutrient balance and growth-differentiation balance hypotheses for two co-occurring classes of plant defense. PloS ONE 7: e47554. CrossRef

Matsubayashi, K. W., Ohshima, I. and P. Nosil. 2010. Ecological speciation in phytophagous insects. Entomologia Experimentalis et Applicata 134: 1-27. CrossRef

Misiewicz, T.M. and P.V.A. Fine. 2014. Evidence for ecological divergence across a mosaic of soil types in an Amazonian tropical tree: *Protium subserratum* (Burseraceae). Molecular Ecology 23: 2543-2558. CrossRef

Nosil, P., Egan, S.P. and D. J. Funk. 2008. Heterogeneous genomic differentiation between walking-stick ecotypes: “isolation by adaptation” and multiple roles for divergent selection. Evolution 62: 316-336. CrossRef

Nosil, P. 2012. Ecological speciation. Oxford Univeristy Press, New York, New York. CrossRef

Powell, T. H. Q., Hood, G. R., Murphy, M.O., Heilveil, J. S., Berlocher, S.H., Nosil, P. and J. L. Feder. 2013. Genetic divergence along the speciation continuum: the transition from host race to species in Rhagoletis (Diptera: Tephritidae). Evolution 67: 2561-2576. CrossRef

Richards, L.A., Dyer, L.A., Smilanich, A.M. and Dodson, C.D. 2010. Synergistic effects of amides from two Piper species on generalist and specialist herbivores. Journal of Chemical Ecology 36: 1105-1113. CrossRef

Richards, L.A., Dyer, L.A., Forister, M.L., Smilanich, A.M., Dodson, C.D., Leonard, M.D. and C.S. Jeffrey. 2015. Phytochemical diversity drives plant–insect community diversity. PNAS 112: 10973-10978. CrossRef

Ricklefs, R.E. 1977. Environmental heterogeneity and plant species diversity: a hypothesis. The American Naturalist 111: 376-381. CrossRef

Rundle, H. D., Nagel, L., Boughman, J. W. and D. Schluter. 2000. Natural selection and parallel speciation in sympatric sticklebacks. Science 287: 306-308. CrossRef

Rundle, H. D. and P. Nosil. 2005. Ecological speciation. Ecology Letters 8: 336-352. CrossRef

Schluter, D. and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. American Naturalist 140: 85-108. CrossRef

Schweitzer, J.A., Juric, I., van der Voorde, T.F.J., Clay, K., van der Putten, W.H., Bailey, J.K. 2014. Are there evolutionary consequences of plant-soil feedbacks along soil gradients? Functional Ecology 28:55-64. CrossRef

Smilanich, A.M., Dyer, L.A., Chambers, J.Q. and M.D. Bowers. 2009. Immunological cost of chemical defence and the evolution of herbivore diet breadth. Ecology Letters 12: 612-621. CrossRef

Smilanich, A.M., Fincher, R.M. and L.A. Dyer. 2016. Does plant apparency matter? Thirty years of data provide limited support but reveal clear patterns of the effects of plant chemistry on herbivores. New Phytologist 210: 1044-1057. CrossRef

Soria-Carrasco, V., Gompert, Z., Comeault, A. A., Farkas, T. E., Parchman, T. L., Johnston, J. S. et al. 2014. Stick insect genomes reveal natural selection's role in parallel speciation. Science 344: 738-742. CrossRef

Sollins, P., Sancho, F.M., Mata, R. and R.J. Sanford. 1994. Soils and soil process research. *In* McDade, L.A., K.S. Bawa, H.A. Hespenheide, and G.S. Hartshorn (Eds). La Selva: Ecology and Natural History of a Neotropical Rainforest, pp. 34-53. University of Chicago Press, Chicago, Illinois.

Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. The Quarterly Review of Biology 78: 23-55. CrossRef

Stireman III, J. O., Nason, J. D. and S.B. Heard. 2005. Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. Evolution, 59:2573-2587. CrossRef

Thompson JN. 1999. Specific hypotheses on the geographic mosaic of coevolution. American Naturalist 153: S1-S14. CrossRef

Thompson JN. 2005. The geographic mosaic of coevolution: University of Chicago Press.

van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T. et al. 2013. Plant-soil feedbacks: the past, the present, and future challenges. Journal of Ecology 101:265-276. CrossRef

van Breeman, N. and A.C. Finzi. 1998. Plant-soil interactions: Ecological aspects and evolutionary implications. Biogeochemistry 42: 1-19. CrossRef

Waddington, C.H. 1953. Genetic assimilation of an acquired character. Evolution 7: 118-126. CrossRef

Ward, M., Dick, C.W., Gribel, R. and A.J. Lowe. 2005. To self, or not to self… A review of outcrossing and pollen-mediated gene flow in neotropical trees. Heredity 95: 246-254. CrossRef

West-Eberhard, M.J. 2003. Developmental plasticity and evolution. Oxford University Press, New York, New York.

Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. Nature Reviews Genetics, 7: 510-523. CrossRef

Whitham, T.G., DiFazio, S.P., Schweitzer, J.A., Shuster, S.M. Allan, G.J., Bailey, J.K. et al. 2008. Extending genomics to natural communities and ecosystems. Science 320: 492-495. CrossRef

Wilson, J. S., Forister, M.L., Dyer, L.A., O'Connor, J.M., Burls, K., Feldman, C.R. et al. 2012. Host conservatism, host shifts and diversification across three trophic levels in two Neotropical forests. Journal of Evolution Biology 25: 532-546. CrossRef