

## Review Article

# Of “Host Forms” and Host Races: Terminological Issues in Ecological Speciation

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Successful communication and accurate inferences in science depend on the common understanding and consistent usage of the terms we apply to concepts of interest. Likewise, new terminology is required when important concepts have gone unnamed. Here, I focus on terminological issues about biological variation and ecological speciation, especially in herbivorous insects but also more generally. I call for the more restricted use of concepts that have sometimes been misapplied, and thus caution against synonymizing ecological speciation with sympatric speciation and the unwarranted invocation of “host races” to describe herbivorous insect differentiation. I also call for the qualified application of terms for different kinds of biological variation and for host range when confronting uncertainty. Among other “missing terms” introduced here is “host form,” a generic term describing any case of host-associated differences for which current evidence does not allow diagnosis of the specific kind of variation. Embracing the use of host form should free host race from its current overapplication. Finally, I present a case study in which *Neochlamisus* leaf beetle populations previously described as host forms are hereby declared to be host races, based on accumulated evidence supporting each of the associated criteria.

## 1. Introduction

A rose by any other name may indeed smell as sweet. However, if a rose vendor started advertising his product as “ragweed,” he would find himself selling fewer flowers. And if a biologist unfamiliar with ragweed purchased his wares for analysis, they would come to different conclusions than had they collected actual ragweed in the field. Words, after all, are imbued with the meanings we assign to them. In science, effective communication entails that terms have well-defined and consistently used meanings and that new terms be created as needed to describe unlabelled concepts. In a field as concept-driven as evolutionary biology [1, 2], maintaining a one-to-one relationship between terms and meanings is especially critical. Indeed, our rose merchant’s application of a different “common name” to his roses need not have confused our biologist if their scientific name was also on display. This is because Linnaeus’s stratagem of applying a unique Latin binomial to every species [3] provided a common and specific language that eliminated confusion about

what organism two people might be discussing, even if they differed in nationality or native tongue.

The Linnaean system of binomials continues to be usefully applied today. However, the typological view of species on which it was based primarily retains its utility for the taxonomist. Following Darwin’s Origin [4], the typologist’s notion of species as largely invariant and discretely different entities gave way to a population-oriented view that embraced continuous intraspecific variation and invoked reproductive barriers to genetic exchange to explain how species remained differentiated from each other [5]. This “population thinking” and the associated biological species concept promoted the recognition of various kinds of biological variation within and around the species level and the consideration of how they relate to species diagnosis and the process of speciation [5]. For example, the entomologist Benjamin Walsh recognized quite early that causal relationships likely existed among the host plant associations of herbivorous insects, their patterns of phenotypic variation, their opportunities for interbreeding, and their species status.

He thus spoke of “phytophagous varieties” and “phytophagous species” [6]. In so doing, Walsh began a long tradition of using herbivorous insects as exemplars of different kinds of biological variation [7–10] and for the study of speciation [2, 22, and 34]. Most recently, insect herbivores have provided many of the best-documented examples of what has become known as ecological speciation [11, 12].

Here I address outstanding terminological issues that affect our understanding of biological variation and ecological speciation and that are currently in need of attention. In illustrating such issues I focus largely on herbivorous insects for the reasons given above. That said, I additionally introduce new terms that are applicable to all taxa. A major goal is to demonstrate that, far from being merely semantic in nature, terminological shortcomings have important consequences for how we view central issues in speciation. I thus further call for the careful and specified use and creation of terms. I do not, however, chronicle and count up cases of terminological misuse in the literature to support my assertions of their existence. I do not wish to unfairly single out particular authors for misnomers common to others. And I do not believe that a more systematic evaluation of misuse frequencies is necessary to argue the value of a more stringent use of terms. Rather I hope that by considering the points made here the reader will develop a more critical eye in reading and writing the associated literature, to the betterment of speciation studies.

## 2. Ecological Speciation ≠ Sympatric Speciation

To begin let us consider a recurring misuse of “ecological speciation” itself. First I give some background.

For much of the 20th century a principal focus of speciation studies was determining the geographic context in which speciation occurred and the relative efficacy of different contexts for facilitating this process [13]. An issue of special concern was how readily populations could speciate in the absence of geographic isolation (allopatry), with the view becoming dominant that nonallopatric, “speciation with gene flow,” modes were difficult and rare [13]. Sympatric speciation received special scrutiny as it required that reproductively isolated populations evolve from within an initially panmictic population in the face of opportunities for homogenization by the countervailing forces of gene flow and recombination. Thus, while enthusiasm for sympatric speciation has continued to wax and wane, it is generally accepted to be a theoretically more onerous mode than allopatric speciation and thus to require quite particular conditions for its occurrence [14, 15].

Toward the end of the 20th century, debates about geographic modes had to make room for an emerging interest in the causes of reproductive isolation per se, and especially in the potential contributions of ecological adaptation and sexual selection. The term “ecological speciation” was coined to describe the evolution of reproductive isolation as an incidental consequence of divergent adaptation to alternative environments, due to the pleiotropic effects of selected genes, or the direct effects of genes tightly linked to them, on traits involved in reproductive isolation [16, 17]. As experimental

and comparative evidence for the association of ecological traits with reproductive isolation accumulated, ecological speciation gained support as an evolutionarily important process and has induced little controversy [18, 19] but see [20].

Critically, ecological speciation is not dependent on geographic context. So long as reproductive isolation is evolving as a consequence of divergent adaptation, ecologically speciating populations could be completely allopatric on separate islands or completely sympatric, living on different plant species intermingling in the same field. Similarly, sympatric speciation may depend on ecological differentiation, or alternatively on sexual selection or polyploidy [21]. Thus, ecological speciation and sympatric speciation incompletely overlap in the cases of speciation they circumscribe [22]. Nonetheless, the intermingling plant scenario exemplifies the reliance of many models of sympatric speciation on the ecological divergence of newly formed subpopulations. And if indeed sympatric speciation is rarer than allopatric speciation and most commonly involves ecological divergence, then most cases of sympatric speciation will also represent ecological speciation, while only a minority of ecological speciation scenarios will involve sympatric speciation.

Despite this asymmetry, ecological speciation is sometimes equated (conflated) with sympatric speciation in the literature. Sometimes an association between ecological divergence and reproductive isolation is taken as de facto evidence for sympatric speciation in the absence of support for sympatric origins. This presumably occurs because the commonly ecological basis of sympatric speciation has forged a false equivalency between ecological causes of reproductive isolation and sympatric speciation in the minds of some workers. In the extreme, the term ecological speciation itself is sometimes coopted as a synonym for sympatric speciation and even erroneously contrasted with allopatric speciation.

This terminological misuse is important as it contributes to misunderstanding about the relative frequency of speciation mechanisms. Ecological speciation per se is theoretically simple and straightforward, and abundant empirical evidence now supports it [18], while conditions for sympatric speciation are theoretically restrictive and evidence compellingly supporting it—regardless of how common it may actually be—is difficult to obtain [14]. Thus, conceptually equating these terms makes sympatric speciation appear to be more broadly supported than it actually is.

## 3. The Kinds of Biological Variation

Speciation is a population-level process with many stages, and species are heterogeneous entities. Thus, their study requires a lexicon of terms describing variation at the individual, population, and species levels, one that is sufficient to describe any case of biological variation. In herbivorous insects, these kinds of variation are often host specific. They may also be cryptic, as host adaptation may be behaviorally or physiologically rather than morphologically based. Not for nothing were herbivorous insects focal subjects for early discussions of sibling species [7, 8] and later evaluations of intraspecific ecological heterogeneity [23]. These many

sources of variation led to terminological confusion and a need for clear distinctions [10]. The following list of terms is a bit entomocentric and is not comprehensive (missing, e.g., various infraspecific botanical terms), but should nonetheless allow for the assignment of differences between two organisms of any taxon to one or more kinds of biological variation.

*Species.* A contentious term with many suggested definitions (i.e., concepts; see [21]). These generally describe a set of populations that is reproductively, historically, genetically, and/or ecologically distinct from other such populations. The biological species concept, whereby species are groups of actually or potentially interbreeding populations that are reproductively isolated from other such groups, remains the most frequently adopted definition by evolutionary biologists.

*Sibling species (sensu [13]) = cryptic species.* Biological species that are approximately anatomically identical to each other. Herbivore sibling species are commonly associated with different host plants.

*Hybrids (sensu [24]).* The products of interbreeding between differentiated populations or separate species.

*Geographic races = subspecies (cf. [24]).* Geographically distinct populations exhibiting genetically based phenotypic differences. Subspecies are essentially geographic races with formal taxonomic status.

*Ecotypes (sensu [25]) (related to the above).* Spatially distinct populations exhibiting divergent adaptation to alternative environments. Herbivores adapted to different host plants in different areas are an example.

*Host races (sensu [26]).* Sympatric populations that are incompletely reproductively isolated but remain ecologically differentiated in the face of gene flow due to divergent selection on populations using alternative hosts. Generally applied to herbivores, but sometimes to other parasites. The diagnosis of host races is discussed below.

*Sympatric races.* A “missing term” (coined here) completely analogous to host races but applied to populations of any taxon—namely, nonparasitic ones—using analogous criteria.

*Populations (sensu [13]).* Ideally, panmictic groups of individuals. More commonly used to refer to spatially coherent groups of potentially interbreeding individuals that exhibit reduced migration and thus potential genetic differentiation.

*Envirotypes.* A “missing term” (coined here) referring to populations or individuals that differ in phenotype due to differences in environmental rather than genetic factors, that is, reflecting phenotypic plasticity. Examples are provided by

induced differences between conspecific herbivores as a function of the different host plants on which they developed.

*Morphs (sensu [13]).* Discrete phenotypic variants that segregate within a population.

*Polymorphisms (sensu [27]).* Multiple genetic variants, often segregating within a population (includes morphs).

*Biotypes (sensu [10]).* The set of herbivorous insect individuals that share the same genotype at given loci of interest and thus phenotypically differ from other biotypes. Most often used in reference to different insect herbivore genotypes, each adapted to use a different host plant genotype.

*Sexual dimorphism.* Phenotypic differentiation between the sexes within a population.

*Developmental variation.* Differences in phenotype reflecting different stages of individual development or of a complex life cycle.

*Host forms.* A “missing term” (coined here) for groups of herbivore individuals or populations exhibiting host-associated biological variation, but where the kind of variation has not yet been diagnosed.

*Ecological forms.* A “missing term” (coined here) completely analogous to host forms but appropriately applied to members of any taxon—namely, nonparasitic ones—that exhibit habitat-or resource-associated differentiation.

Excepting host races, discussed below, means of diagnosing these kinds of variation are not described here.

## 4. Nominal Host Ranges

For insect herbivores another sort of variation is critical for understanding ecological speciation: host range, that is, the number, identity, and relatedness of host plant taxa [28]. Variation in host range is described by its own suite of terms. A “narrow” host range includes few and/or closely related hosts, while a “broad” host range includes many and/or distantly related host taxa. The narrower its host range, the more “specialized” a herbivore is said to be, with insects using a single host taxon being described as “monophagous.” The broader the host range, the more “generalized” or “polyphagous” the herbivore is said to be. Herbivores using several host taxa are referred to as “oligophagous.”

An accurate understanding of a herbivore’s host range is crucial to studying host-associated ecological speciation. Notably, most such examples involve highly specialized populations that are divergently adapted to alternative host plant species [11, 12]. Thus, one might predict a greater tendency towards specialization in a herbivore group to be associated with a greater tendency towards ecological speciation, via host shift and subsequent adaptation to the new host. One might also predict a herbivore taxon whose

species tend to specialize on distantly related host plants to be more prone to ecological speciation than one whose species all use closely related hosts. This is because host shifts between more biologically divergent hosts will likely incur more strongly divergent selection, resulting in concomitantly large increases in reproductive isolation [29]. *Neochlamisus* leaf beetles, my focal study system, provide an example of both of these tendencies. Species in this genus usually specialize on a single host genus or species, with these hosts broadly scattered across eudicot phylogeny [29]. Following the above predictions, the only *Neochlamisus* species that regularly uses multiple (six) different and distantly related host genera/species, *N. bebbiana*, exhibits pronounced host-associated ecological divergence and reproductive isolation between populations affiliated with different hosts [29]. In this example, what was described as an oligophagous species [30] was experimentally proven not to be composed of populations with similar oligophagous tendencies, but rather of a complex of divergently host-specialized populations, each accepting its native host (i.e., the one used in nature) more readily than the five plants used by other populations [31].

The case of *N. bebbiana* not only illustrates why accurately assessing host range is vital to understanding ecological speciation but also why many herbivore host ranges are likely to be inaccurately or incompletely documented. Identifying the particular suite of hosts used by a given species or population requires intensive fieldwork. This includes the inspection of presumed nonhosts cooccurring with documented hosts, to determine if host range is broader than presumed. It further requires evidence that a “documented” host is indeed actively used as resource rather than simply being a place of temporary rest by an insect “tourist,” in which case the actual host range is narrower than presumed. Moreover, as with *N. bebbiana*, experimental work is needed to identify possible cryptic variation in host use, that is, whether a nominal species is actually subdivided into a complex of populations or sibling species with divergent host ranges. Thus, determining host range requires determining the kind of biological variation one is studying. For herbivores that have not been studied in this comprehensive manner, the potential for ambiguity might be usefully highlighted by speaking of a “nominal” host range. Acknowledging such ambiguity is critical as host range bears not only on ecological speciation but also on the evolution of ecological specialization, the macroevolutionary dynamics of host use, crop pest control strategies, and so forth (e.g., [32, 33]).

Note that these terms and issues may analogously be applied to the host range of nonherbivore parasites or to the “ecological range” of nonparasitic taxa.

## 5. “Host Form”: A Missing Term in the Vocabulary of Biological Variation

Just as it is important to recognize when one has an incomplete understanding of host range, it is vital to assess confidence in one’s assessment of the kind of biological variation being addressed and to acknowledge the lack of same. Presuming the kind of variation one is dealing with without

sufficient evidence to rule out alternatives risks an erroneous diagnosis while compromising inferences premised on the kind of variation at hand. For example, if different envirotypes are instead presumed to be host races or separate species, associated conclusions about speciation processes will be erroneous. As in the case of host range, a problem that promotes such misinterpretations is a current vocabulary that is insufficient to describe uncertainties. And a lack of terms indicating ambiguity may encourage workers to be less circumspect and make a best guess as to the kind of variation at hand in the absence of sufficient evidence. As suggested for host range, one could simply qualify uncertain assignments as “nominal.” A more conservative approach might, however, be advantageous, especially in the frequent situations where variation along host plant lines has been documented, but current evidence is limited and remains consistent with multiple kinds of variation. The term “biotype” used to be rather haphazardly applied to diverse kinds of variation [10]. But this owed to a lack of consensus on the meaning of that term rather than to a conscious effort to indicate uncertainty. In recent years, workers have begun writing about “host-associated differentiation (HAD),” a more general and somewhat variably applied term recently defined by Dickey and Medina [34] as, “the formation of genetically divergent host-associated sub-populations.” However, this term is not broad enough to span all kinds of biological variation and describes the relationship between populations rather than the populations themselves.

It seems then that the field is missing what would be a valuable term, one that allowed workers to acknowledge the existence of host-associated variation, while remaining neutral on the kind of variation it represents. The creation of such a term would eliminate the necessity of guesswork while recognizing a phenomenon of interest and pointing it out as needing additional study.

Thus, *host forms* = groups of individuals or populations exhibiting host-associated biological variation, but where the kind of variation has not yet been diagnosed.

I am formally introducing this term for the first time here. That fact notwithstanding, I have used it in prior publications when referring to the populations of *N. bebbiana* leaf beetles associated with their six different host plants [11, 29, 31, 35–42]. As my prior use of “host form” in papers and talks has not led to its broader adoption by the field, I hope that this paper will more effectively encourage such usage (!). The coining of this term was motivated by three things: first, the demonstration of cryptic host-associated variation within *N. bebbiana*, namely, patterns of relative acceptance of the six *N. bebbiana* hosts that varied according to the native host of the test population [31]. Second, insufficient data to infer what kind of biological variation was represented by beetles natively associated with each of the six hosts. Third, the lack of an existing term suitable for describing this real yet underdetermined kind of host-associated variation. Thus, I coined “host form” as an evolutionarily neutral and needed missing term in the vocabulary of biological variation. I have also introduced “ecological form” as an analogously neutral term to be applied to underinvestigated nonparasitic taxa exhibiting some form of ecological differentiation.

## 6. Host Races: Ever Intriguing, Overdiagnosed

Among the different kinds of biological variation, host races might be argued to be the most intriguing, at least to students of speciation. The reasons are twofold (see [21, 26, 43], for discussion of the following issues). First, host races represent intermediate points along the speciation continuum and thus provide unusual opportunities for studying speciation as a process. This is because host races exhibit considerable but incomplete reproductive isolation. This reproductive isolation, in concert with divergent selection, can facilitate or maintain ecological differentiation between host races and genomic differentiation at regions under sufficiently strong divergent selection. The gene flow that does occur prevents the fixation of alternative alleles even at selected loci, while homogenizing the majority of the genome between populations (see, e.g., [44]). However, whether host races will continue along the path to speciation, remain indefinitely at an equilibrium level of differentiation, or ultimately collapse back into a single population is never known.

Second, because host races demonstrate that adaptive differentiation and partial reproductive isolation can be maintained in the face of local gene flow, they have long been offered as evidence for the plausibility of sympatric speciation (e.g., [9]). This is important because, as noted earlier, the theoretical conditions under which sympatric speciation can occur are generally restrictive. However, although the existence of host races is consistent with sympatric speciation, it does not imply sympatric speciation. Indeed, the most theoretically onerous stages of sympatric speciation are the early ones in which reproductive isolation must evolve from within an initially panmictic population [14]. Thus, unless sympatric origins have been demonstrated, host races may alternatively reflect secondary contact and the maintenance of differentiation between populations whose initial divergence occurred allopatrically. Nonetheless, an erroneous bond between these terms can be found in the literature whereby claims of host race status are implicitly or explicitly linked with an inference of sympatric speciation. This bond may have promoted an overestimation of how amply sympatric speciation has been documented. This is somewhat similar to how the overlap between ecological speciation and sympatric speciation has led to inappropriate equating of these concepts and an overestimate of the latter.

To take this argument back a step, a greater problem is a considerable overdiagnosis of host races themselves that runs boldly through the literature. This despite a long history of delineating the criteria for host race status [10, 13, 45], culminating in an especially well-detailed and argued characterization of these criteria [26]. According to Drès and Mallet, host races are sets of populations with the following characteristics. (1a) They use different host taxa in the wild and (1b) consist of individuals that exhibit host fidelity to their respective hosts. (2) They coexist in sympatry in at least part of their range. (3a) They are genetically differentiated at more than one locus and (3b) are more genetically differentiated from each other in sympatry than either is from some geographically distant populations on the same host. (4a) They display a correlation between host choice and

mate choice and (4b) undergo appreciable gene flow. (5a) They have higher fitness on natal than alternative hosts and (5b) produce hybrids that are less fit than parental forms. (Note that analogous criteria must be met for populations of nonherbivorous parasites to be appropriately assigned host race status or for nonparasites to be assigned sympatric race status.) The authors apply these criteria to the literature in search of study systems that qualify as host races. Notably, this search turned up only three such systems, and even these are listed as uncertain for criterion (5b). This number is strikingly low. And even if the ten years since this paper's publication has seen the documentation of more such cases, it seems unlikely that compelling evidence for host races is nearly as common as their invocation in the literature would imply. Surely this term is being misapplied. Why so?

Three related reasons come to mind. First, consider again that sympatric speciation is theoretically onerous and thus often argued to be rare and also that understanding patterns of diversification (e.g., the spatial coexistence of related species) would be much simpler should this speciation mode be plausibly frequent. For these reasons, evidence supporting sympatric speciation is rightly greeted with special excitement. Consider again too that evidence for host races is sometimes considered de facto evidence for sympatric speciation. Due to this connection, then, work claiming host race documentation might also be viewed as especially noteworthy, above and beyond the intrigue rightly accorded to host races per se. Because journals seek to publish important and broadly interesting findings, a selection process may thus be inadvertently imposed that favors the publication of such work and thus the making of such claims. Somewhat conversely, a second reason may be that as the plausibility of sympatric speciation has become more widely accepted in recent years ([46], e.g., announces its comeback) so has the plausibility of host races, again by virtue of their perceived equivalence. Presuming the veracity of this view, there may be every good reason, from the perspective of likelihood, to suspect that a case of host-associated differentiation could potentially be a case of host race formation. Thus, data consistent with, if not specifically demonstrative of, host races may more likely be used as the basis for a paper focusing on hopeful host races. The third reason is based on what sometimes appears to be the invocation of host races without any apparent justification. Here, it might be suspected that workers have simply not familiarized themselves with the criteria for diagnosing host races and that their frequent invocation has, via a positive feedback loop, resulted in such haphazard use as to make this term almost synonymous with host-associated variation per se. That is, it appears that in some circles this most intriguing and empirically onerous term is now serving the purpose of the least restrictive of terms, that of the here-proposed "host form." This explanation might account for my own experiences of having *N. bebbiana* populations that I have consistently referred to as "host forms" nevertheless described in paper and grant reviews as "host races." Hopefully, the introduction of host form into the vocabulary of biological variation will help restore host race to its proper place as an inherently fascinating phenomenon and a more reluctantly invoked term.

## 7. From Host Forms to Host Races: The Maple- and Willow-Associated Populations of *N. bebbiana*

Readers to this point may suspect that I hold views antithetical to the notions of host races and sympatric speciation. Rather, I am fairly agnostic on the issue of how evolutionarily frequent and important these phenomena are. Indeed, recent population genomic work may herald the common documentation of adaptive genomic differentiation in the face of gene flow [42]. However, just as Drès and Mallet [26] have provided criteria for documenting host races that seldom seem to have been demonstrated, so too does sympatric speciation theory lay out predicted parameters that have rarely been estimated [15]. Part of the problem is undoubtedly that obtaining adequate data for any one system requires a great amount of work. And sealing a strong case for sympatric speciation requires information—on the historical distributions of populations/species—that is rarely available. The latter point may forever prohibit claims about sympatric speciation (pro or con) in my focal study system, *Neochlamisus* leaf beetles. However, work on two of the six *N. bebbiana* host forms, those associated with maple and willow, has by now given me sufficient confidence to cease my use of “host forms” to describe these populations and declare, here, that they represent proper host races. Following the criteria of Drès and Mallet [26], the findings on which this claim is based are as follows.

(1a) These host forms are associated with divergent host taxa in nature, using red maple (*Acer rubrum*, Aceraceae) and Bebb's willow (*Salix bebbiana*, Salicaceae), respectively [35].

(1b) Choice experiments involving<sup>6</sup> host cuttings in salad containers and leaf fragments in Petri dishes demonstrate that each sex of both host forms spends the majority of its time on its native host, demonstrating host fidelity [35].

(2) These host forms coexist in sympatry and syntopy in the same disturbed and riparian habitats across a broad region of northeastern North America (New England, New York, and southeastern Canada), where they commonly grow intermixed with each other. For example, I have documented host-associated differentiation in sympatric populations from Cumberland Co., ME, Kennebec Co., ME, Middlesex Co., MA, Exeter Co., NH, Oswego Co., NY (from 2 different sites), and Caledonia Co., VT.

(3a) Genome scan data reveal multiple loci that are much more highly differentiated than expected under drift [44]. Many of these putatively divergently selected “outlier” loci are only differentiated in comparisons of populations using different hosts, implicating them in divergent host adaptation. Notably, this differentiation is observed between sympatric populations of the host forms from a site in northern Vermont.

(3b) Population trees based on these host-associated outlier loci show these sympatric host forms to be more differentiated from each other than either is to allopatric populations of the same host form [44].

(4a) The host fidelity of these host forms is associated with mating fidelity, in that positively assortative mating (= sexual isolation) is observed between them, with each one

mating more readily with individuals of the same host form [11, 35].

(4b) Population trees based on putatively neutral loci group the sympatric populations together as more genetically similar to each other than either is to allopatric populations of the same host form, as expected if gene flow has homogenized neutral loci in sympatry [44].

(5a) Each host form grows faster and survives better on its native host than on the host of the other host form [35, 41, 47].

(5b) Hybrids between these host forms exhibit reduced growth rate and survivorship than the parental types do on their native hosts [41, 47].

*N. bebbiana* thus presents one of the very few examples for which data meet all the criteria of host races. They also more generally represent an increasingly well-understood case of potentially ongoing ecological speciation.

## 8. Conclusion

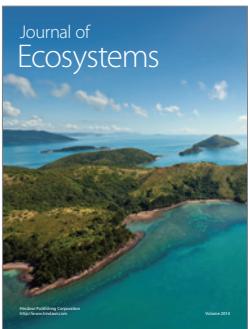
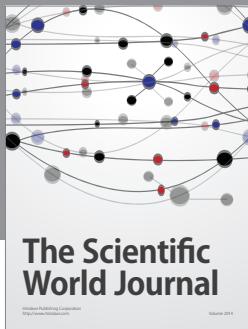
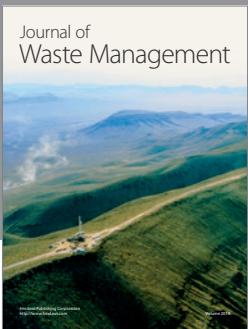
As does any form of rigorous inquiry, the accurate, informed study of ecological speciation depends crucially on terminological issues. It requires that terms be used in a manner consistent with their definitions. It requires that terms be qualified as necessary to accurately convey degree of confidence. It requires that “missing” terms be created as needed to fill conceptual gaps. It requires that inappropriate synonymizing, loose usage, and simple terminological ignorance be avoided. As argued here, deviations from these prescriptions seem to have led to overestimation of the evidence supporting host races and sympatric speciation, and the diffusion of the former term's special status as an important evolutionary phenomenon. This loss may owe to the prior lack of an alternative term to convey the existence of host-differentiated entities whose evolutionary status cannot yet be determined. Such a term, “host form,” is proposed here as an important conceptual gap-filler. By contrast, the proper application of the term host race is illustrated here by describing how each of its criteria are fulfilled by maple- and willow-associated populations of *N. bebbiana* leaf beetles. Although the focus of this paper has been on herbivorous insects, the appropriate application of (sometimes new) terms and concepts across diverse taxa is also highlighted.

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